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NEW CALEDONIAN CHAROPID LAND SNAILS. I. REVISION OF THE GENUS *PARARHYTIDA* (GASTROPODA: CHAROPIDAE)

Peter Mordan[1] & Simon Tillier[2]

ABSTRACT

Six species of the charopid genus *Pararhytida*, three of them previously undescribed, are recognised in a taxonomic revision based on material from 72 sites.

Pararhytida is endemic to New Caledonia, being found in most areas of primary forest on the mainland, as well as the Belep Islands. It appears to be absent from the Loyalty Islands and earlier records from the Isle of Pines are not confirmed. Whereas the largest species, *P. dictyodes*, occurs throughout the mainland, the remaining species are more restricted in distribution.

The occurrence of spermatophores in the Charopidae is recorded for the first time.

Key words: Charopidae; *Pararhytida*; taxonomy; New Caledonia.

INTRODUCTION

The endemic New Caledonian charopid genus *Pararhytida*, previously revised by Franc (1956) and Solem (1961) on a purely conchological basis, is remarkable in several respects:
1. One species reaches 37 mm in shell diameter, exceeding the size of any other known endodontoid. 2. Part of the dorsal surface of the tail is thickened to form a pseudo-operculum, a structure analogous to the operculum of prosobranchs and some lower pulmonates, and known elsewhere only in the related New Caledonian genus *Rhytidopsis* Ancey. 3. Sperm is exchanged in a horny spermatophore, which in some species is strikingly similar in morphology to that of helicarionid snails. Although previously unrecorded in endodontoids, the occurence of a horny spermatophore is common in New Caledonian charopids, but only in *Pararhytida* is it formed of a fusiform body prolonged as a thin, denticulate tail.

Six species of *Pararhytida* are recognised in the present paper, three of them being described as new: *Pararhytida dictyodes* (Pfeiffer), the type species; *P. mouensis* (Crosse); *P. marteli* (Dautzenberg); *P. phacoides* n.sp., *P. pyrosticta* n.sp. and *P. thyrophora* n.sp. One of the four species recognised by both Franc (1956) and Solem (1961), *P. dictyonina* (Euthyme), is synonymised with *P. mouensis*. Species belonging to *Micromphalia* Ancey, 1882, and *Plesiopsis* Ancey, 1888, treated by both Franc and Solem as subgenera of *Pararhytida*, are excluded from the genus. *Tropidotropis gudei* Preston, 1907, considered by Solem (1961) to be a synonym of *T. trichocoma* (Crosse), is a juvenile *Pararhytida mouensis*.

This study is based on material collected at 72 sites in New Caledonia (Table 1; Fig. 1). Except where otherwise stated, specimens are from the Muséum national d'Histoire naturelle, Paris (MNHN), but some are also from the Field Museum of Natural History, Chicago (FMNH). All the relevant type material is housed in either the MNHN or the British Museum (Natural History), London (BMNH) and has been examined.

DISTRIBUTION AND ECOLOGY

Pararhytida is found in almost all the mainland areas of New Caledonia where primary forest remains, as well as the Belep Islands, but is apparently absent from the Loyalty Islands. We do not record *Pararhytida* from the Isle of Pines, although both Crosse (1894) and Franc (1956) mention *P. dictyodes* from there; this may be due to insufficient collecting by us.

[1]Department of Zoology, British Museum (Natural History), London SW7 5BD, England.
[2]Laboratoire de Biologie des Invertébrés marins et Malacologie, Muséum national d'Histoire naturelle, 55 rue Buffon, F-75005 Paris, France.

TABLE 1. List of sampling stations.

5. Le Cresson, 164° 18′ 36″ E; 20° 29° 00″ S. 100 m, dry forest on calcareous outcrop. Rainfall 1200 mm. A. & S. Tillier coll., 30.vi.1979. *P. dictyodes:* 3a + 23s. P. Mordan, A. & S. Tillier coll., 29.i.1981. *P. dictyodes:* 1s + 1 juv. a + 1 juv. s. Probably *idem.* FMNH 159259, L. Price coll. *P. dictyodes:* 17a + 1s.

6. Grottes de Koumac, 164° 20′ 27″ E; 20° 31′ 52″ S. 80 m, dry forest on calcareous outcrop. Rainfall 1200 mm. P. Bouchet coll., 14–15.vi.1978. *P. dictyodes:* 11s + 1 juv. a + 5 juv. or broken. A. & S. Tillier coll. 30.vi.1979. *P. dictyodes:* 3s + 3 juv. s + 2 juv. a. P. Mordan, A. & S. Tillier coll., 29.i.1981. *P. dictyodes:* 6s + 2 juv. s.

7. Mandjelia, 14° 30′ 06″ E; 20° 22′ 29″ S. 400 m, 5 km N of sawmill, rainforest. Rainfall 1900 mm. A & S. Tillier coll., 2.vii.1979. *P. dictyodes:* 2a.

9. Ruisseau de l'Etoile du Nord (Oue Paoulou), 164° 20′ 27″ E; 20° 34′ 48″ S. 150 m, dry forest, probably on a calcareous outcrop. Rainfall 1200 mm. A & S. Tillier coll., 30.vi.1979. *P. dictyodes:* 2s.

12. Mt. Taom, 164° 34′ 45″ E; 20° 46′ 55″ S. 900 m, altitude rainforest in a thalweg, on ultrabasic rock. Rainfall 2500 mm. A. & S. Tillier coll. 30.vi.1979. *P. dictyodes:* 5s + 1 juv. s. + 1 juv a. (SEM).

14. Momies de la Fatenaoué, S side Mt. Tende, 164° 43′ 22″ E; 20° 52′ 36″ S. 100–200 m, dry forest. Rainfall 1250 mm. A. & S. Tillier coll. 4.vii.1979. *P. dictyodes:* 2s.

16. Plateau de Tango, track to Bobeitio, 164° 00′ 27″ E; 20° 58′ 29″ S. 300–350 m, rainforest. Rainfall 1800 mm. P. Bouchet coll. 24.xii.1978. *P. dictyodes:* 1s + 1 juv. s + 2 broken + 1 juv. a.

18. Goipin, 165° 16′ 30″ E; 21° 13′ 19″ S. 50–150 m, rainforest. P. Bouchet coll. 6.v.1979. *P. dictyodes:* 5s.

19. Forêt Plate, 165° 06′ 23″ E; 21° 08′ 57″ S. 540 m, NE slope Mt. Paéoua, rainforest. Rainfall 1841 mm. P. Bouchet, A. & S. Tillier coll. 15.vii.1979. *P. dictyodes:* 1s + 1 juv. s + 1 broken.

20. Mt. Paéoua, 165° 05′ 27″ E; 21° 10′ 48″ S. 950–1000 m, altitude rainforest. Rainfall 3000 mm. A. & S. Tillier coll. 5.vii.1979. *P. dictyodes:* 2a + 3 juv. a + 3 juv. s + 1 broken.

25. Adio, vallée sèche, 165° 14′ 46″ E; 21° 14′ 44″ S. 180 m, dry forest. P. Bouchet coll. 6.v.1979. *P. dictyodes:* 6s + 2 juv. + 1 broken. L. Price coll. 7. xi.1967. FMNH 159309. *P. dictyodes:* 9a + 1 juv. a.

36. Mt. Vulcain, Gallieni mine, 166° 20′ 55″ E; 21° 54′ 33″ S. 700–900 m, maquis. Rainfall 3500 mm. P. Bouchet coll. 5.xii.1978. *P. dictyodes:* 1 juv. s.

37. Mt. Dzumac, 166° 27′ 19″ E; 22° 02′ 30″ S. 950–1000 m, NW of summit, rainforest. Rainfall 3000 mm. P. Bouchet & S. Tillier coll. 4.vi.1979. *P. mouensis:* 1a. *P. dictyodes:* 1 juv. s.

43. Rivière Bleue, 166° 39′ 25″ E; 22° 05′ 47″ S. 160 m, right side of the river, rainforest. Rainfall 2700 mm. P. Bouchet coll. 6.i.1979. *P. mouensis:* 1a. P. Mordan & S. Tillier coll. 29.ii.1981. *P. mouensis:* 3a + 3s.

47. Mt. Guemba, 166° 56′ 10″ E; 22° 10′ 22″ S. 450 m, rainforest. Rainfall 3200 mm. P. Bouchet coll. 10.vi.1978. *P. mouensis:* 1a. *P. marteli:* 1a.

48. Touaourou (St.-Gabriel), 166° 58′ 00″ E; 22° 12′ 00″ S. 10–30 m, rainforest on uplifted coral reef. Rainfall 3000 mm. A. Warén coll. 30.vii.1979 (road to Ni mine, 200 m from main road). *P. marteli:* 1a + 7s + 6s juv. or broken; P. Bouchet coll. 29.v.1978, 8.xii.1978 and 19.vii.1979: *P. marteli:* 4a + 3 a juv. + 9s + 6s juv. or broken.

49. Right side of Kuebeni River, 167° 00′ 07″ E; 22° 16′ 23″ S. 50–80 m, rainforest on ultrabasic rocks. Rainfall 2500 mm. P. Bouchet coll. 12.iv.1979. *P. marteli:* 3a + 7 juv. a + 7s.

50. Goro, 167° 00′ 21″ E; 22° 18′ 57″ S. 30 m, rainforest on ultrabasic rock. Rainfall 1900 mm. P. Bouchet coll. 3.ix.1978. *P. marteli:* 1a.

57. Ile Pott (Belep Islands), S plateau, 163° 16′ 00″ E; 19° 35′ 27″ S. 100–150 m, maquis. Rainfall 1250 mm. P. Bouchet & C. Cherel coll. 27.viii.1978. *P. thyrophora:* 3s.

58. Ile Art (Belep Islands), N plateau, 163° 24′ E; 19° 42′ S. 200–250 m, maquis. Rainfall 1250 mm. P. Bouchet & A. Warén coll. 20.viii.1978. *P. thyrophora:* 13a + 50s + 48 juv. (29a) + 1 broken.

65. Mt. Nindo (near Poum), 164° 10′ 41″ E; 20° 17′ 47″ S. 70 m, gallery forest. Rainfall 1250 mm. P. Bouchet coll. 20.viii.1978. *P. dictyodes:* 3a + 2 juv. a.

66. Col d'Amos, 164° 25′ 20″ E; 20° 18′ 52″ S. 200 m, rainforest. Rainfall 1600 mm. P. Mordan, A. & S. Tillier coll. 31.i.1981. *P. dictyodes:* 17a + 6s + 6s juv. or broken.

69. Mandjelia, 164° 30′ 06″ E; 20° 22′ 29″ S. 550 m, below the sawmill, rainforest. Rainfall 1800 mm. A. & S. Tillier coll. 30.vi.1979. *P. dictyodes:* 1s.

70. Station de Djavel, 164° 23′ 36″ E; 20° 24′ 33″ S. 50 m, secondary dry vegetation. Rainfall 2000 mm. A. & S. Tillier coll. 30.vi.1978. *P. dictyodes:* 4s.

71. Nehoue valley, 164 °16′ 00″ E; 20° 26′ 18″ S. 50 m, dry forest. Rainfall 1300 mm. P. Mordan, A. & S. Tillier coll. 1.ii.1981. *P. dictyodes:* 2a + 11s + 3 juv. (1a).

72. Mt. Ignambi, 164° 36′ E; 20° 27′ S. 850–950 m, rainforest. Rainfall 3000 mm. P. Bouchet coll. 27.xii.1978. *P. pyrosticta:* 1a + 1 juv. a.

74. Colnett, 164° 44′ 24″ E; 20° 29′ 34″ S. 20 m, track to the cascade. Rainfall 4000 mm. P. Mordan & S. Tillier coll. ii.1981. *P. dictyodes:* 1 juv. s.

79. E. slope of Mt. Panié, 164° 48′ 43″ E; 20° 35′ 27″ S. 280 m, rainforest. Rainfall 5100 mm. P. Bouchet & C. Cherel coll. 14.viii.1978. *P. dictyodes:* 1a + 1 juv. a + 1s + 2 juv. s.

80. E. slope of Mt. Panié, 164° 48′ 22″ E; 20° 35′ 54″ S. 580 m, rainforest. Rainfall 5700 mm. P. Bouchet & C. Cherel coll. 14.viii.1978. *P. dictyodes:* 1a + 1 juv. a + 1 juv. s. L. Price coll., 500–700 m, 4. xi.1967. FMNH 159344. *P. dictyodes:* 2a. 900–970 m, rainforest. Rainfall 6400 mm. P. Bouchet & C. Cherel coll. 14.viii.1978. *P. dictyodes:* 2a.

83. Thiem, 165° 06′ 23″ E; 20° 45′ 43″ S. 10–50 m, rainforest. Rainfall 2500 mm. P. Bouchet

coll. 25.xii.1978. *P. dictyodes:* 2a + 12s + 6 juv. a.

84. S. slope of Mt. Tchingou, 165° 00′ 00″ E; 20° 54′ 27″ S. 900–1000 m, rainforest. Rainfall 3000 mm. P. Bouchet, A. & S. Tillier coll. vii.1979. *P. pyrosticta:* 1a + 1s. 1250 m, rainforest. Rainfall 3500 mm. P. Bouchet, A. & S. Tillier coll. vii. 1979. *P. pyrosticta:* 6a + 2s + 6 juv. a + 5 juv. s.

86. N side of Amoa River, 10 km up the valley, 165° 12′ 12″ E; 20° 58′ 00″ S. 20 m, rainforest. Rainfall 2500 mm. P. Bouchet, A. & S. Tillier coll. 12.vii.1978. *P. dictyodes:* 1a. P. Mordan, A. & S. Tillier coll. 18.i.1981. *P. dictyodes:* 1a.

88. S side Mt. Koniambo, 164° 49′ 25″ E; 21° 02′ 00″ S. 600 m, maquis. Rainfall 1500 mm. P. Mordan, A. & S. Tillier coll. 28.i.1981. *P. dictyodes:* 1s.

89. N side of Tchamba River, 5 km up the valley, 165° 19′ 52″ E; 21° 01′ 51″ S. 100 m, forest. Rainfall 2500 mm. P. Mordan, A. & S. Tillier coll. 17.i.1981. *P. dictyodes:* 2s.

91. Mt. Aoupinié, 165° 18′ 00″ E; 21° 10′ 09″ S. 600 m, track above the sawmill, above Goa tribe, rainforest. Rainfall 2700 mm. P. Mordan, A. & S. Tillier coll. 16.i.1981. *P. dictyodes:* 5a + 1 juv. a + 1s + 1 juv. s. *P. pyrosticta:* 1a.

92. Mt. Aoupinié, 165° 15′ 42″ E; 21° 10′ 42″ S. 1000 m, summit area, altitude rainforest. Rainfall 3500 mm. P. Mordan, A. & S. Tillier coll. 16.i.1981. *P. pyrosticta:* 1 juv. a + 2 juv. s.

94. Moneo, 165° 29′ 31″ E; 21° 09′ 36″ S. 10–50 m, rainforest. Rainfall 2500 mm. P. Bouchet coll. 15.v.1978. *P. dictyodes:* 6s + 5 juv. s.

97. Mt. Boulinda, 165° 08′ 57″ E; 21° 14′ 44″ S. 980–1020 m, between Petit and Grand Boulinda, altitude rainforest. Rainfall 3000 mm. A. & S. Tillier coll. 6.vii.1979. *P. dictyodes:* 1s + 1 juv. s. *P. phacoides:* 3a + 1s (broken).

98. Adio caves, 165° 14′ 18″ E; 21° 15′ 36″ S. 180 m, forest on a calcareous outcrop. Rainfall 1400 mm. P. Bouchet & C. Cherel coll. 20.viii.1978. *P. dictyodes:* 1a + 11s + 1 juv. s.

110. S slope of Mt. Table Unio, 165° 45′ 55″ E; 21° 33′ 36″ S. 850–950 m, rainforest. Rainfall 2400 mm. S. Tillier coll. 7.v.1979. *P. dictyodes:* 4a + 1s.

114. Mt. Rembai, 165° 50′ 13″ E; 21° 34′ 54″ S. 800–850 m, N crest, rainforest. Rainfall 2400 mm. S. Tillier coll. 8.vi.1979. *P. dictyodes:* 1a + 2s + 1 juv. a + 1 juv. s.

115. Mt. Canala, 165° 55′ 48″ E; 21° 35′ 00″ S. 900–1050 m, rainforest. Rainfall 2800 mm. P. Bouchet coll. 21.i.1979. *P. dictyodes* 2a.

116. N side Col d'Amieu, 165° 48′ 08″ E; 21° 36′ 00″ S. 400–500 m, W of the Maison Forestière, rainforest. Rainfall 1800 mm. P. Bouchet coll. 18.xi.1978; S. Tillier coll. 7.v.1979. *P. dictyodes:* 2a + 1s + 1 juv. s.

117. Plateau de Dogny, 165° 52′ 33″ E; 21° 36′ 26″ S. 950 m, rainforest. Rainfall 2600 mm. P. Bouchet coll. 1.i.1979. *P. dictyodes:* 1s broken + 1 juv. s.

118. Mt. Nakada, 166° 02′ 26″ E; 21° 38′ 37″ S. 850 m, rainforest. Rainfall 2600 mm. S. Tillier coll. 19.vi.1979. *P. dictyodes:* 6a + 1s + 2 juv. a. *P. phacoides:* 1s + 1 juv. a + 1 juv. s.

119. Mt. Nakada, 166° 03′ 08″ E; 21° 38′ 57″ S. 500 m, above the sawmill, rainforest. Rainfall 2000 mm. S. Tillier coll. vi.1979. *P. dictyodes:* 2a.

123. Mt. Do, 165° 59′ 11″ E; 21° 45′ 30″ S. 950 m, rainforest. Rainfall 2600 mm. P. Bouchet coll. 16.iv.1979. *P. dictyodes:* 1a + 2s + 1 juv. s.

125. Mt. Humboldt, 166° 23′ 29″ E; 21° 53′ 28″ S. 1150 m, crest leading to Mt. Vulcain, rainforest. Rainfall 4500 mm. S. Tillier coll. 22.ii.1981. *P. mouensis:* 1 juv. a.

128. Col de la Ouinné, between Mt. Dzumac and Mt. Ouin, 166° 27′ 54″ E; 22° 01′ 18″ S. 850 m, rainforest. Rainfall 3000 mm. P. Mordan, A. & S. Tillier coll. 25.i.1981. *P. mouensis:* 1a.

130. Mt. Mou, 166° 20′ 34″ E; 22° 03′ 55″ S. 1200 m, altitude rainforest. Rainfall 3400 mm. P. Bouchet & C. Cherel coll. 9.viii.1978. *P. mouensis:* 1 juv. s.

131. Mt. Mou, 166° 19′ 46″ E; 22° 04′ 28″ S. 370–450 m, E of sanatorium, rainforest. Rainfall 1800 mm. P. Bouchet & C. Cherel coll. 5.viii.1978. *P. dictyodes:* 1s + 1 juv. a. P. Mordan, A. & S. Tillier coll. 23.i.1981. *P. dictyodes:* 3s + 2 broken. A. & B. Solem coll. 23.i.1962. FMNH 135440. *P. dictyodes:* 3s.

136. Montagne des Sources, 166° 35′ 56″ E; 22° 07′ 32″ S. 875 m, W slope, rainforest. Rainfall 3500 mm. P. Bouchet, S. Tillier & A. Warén coll. 3.v.1979. *P. mouensis:* 1a + 1s + 2s broken.

140. Mt. Koghi, 166° 30′ 21″ E; 22° 10′ 35″ S. 480–520 m, rainforest. Rainfall 2000 mm. P. Mordan, A. & S. Tillier coll. 10.i.1981. *P. mouensis:* 1a.

142. Col de Mouirange, 166° 39′ 00″ E; 22° 12′ 00″ S. 180–250 m, rainforest. Rainfall 1800 mm. P. Mordan, A. & S. Tillier coll. 11.i.1981. *P. dictyodes:* 1s broken + 1 juv. s. *P. mouensis:* 3a + 3s + 1 juv. a.

143. Col. de Mouirange, 166° 40′ 14″ E; 22° 13′ 19″ S. 200 m, rainforest. Rainfall 1800 mm. S. Tillier coll. 5.vi.1979. *P. dictyodes:* 2s broken.

146. Lac en Y, 166° 55′ 42″ E; 22° 15′ 36″ S. 250 m, maquis. Rainfall 3200 mm. P. Bouchet & S. Tillier coll. 25.vi.1979. *P. dictyodes:* 1 juv. a.

150. Prony, Baie Est, 166° 54′ 11″ E; 22° 22′ 23″ S. 150 m, rainforest. Rainfall 2700 mm. P. Bouchet coll. 10.vi.1978. *P. mouensis:* 1s.

179. Forêt Nord, 166° 53′ 00″ E; 22° 17′ 00″ S. 220–250 m, rainforest. Rainfall 3000 mm. P. Mordan, A. & S. Tillier coll. 24.i.1981. *P. mouensis:* 2a + 3s + 1 broken.

181. Mt. Ningua, 166° 09′ 25″ E; 21° 45′ 17″ S. 950 m, rainforest. Rainfall 2800 mm. S. Tillier coll. vi. 1979. *P. dictyodes:* 1 juv. a + 1s + 1 juv. s. 700 m, rainforest. P. Lespes coll. 10.viii.1979. *P. dictyodes:* 1s (broken).

183. 6 km E of Ouegoa, 140 m. Rainfall 1600 mm. L. Price coll. 1.xi.1967. FMNH 159246 & 159228. *P. dictyodes:* 8a + 2s + 4 juv. a.

184. Bac de la Ouaieme, 0 m, rainforest. Rainfall 3000 mm. P. Bouchet & C. Cherel coll. 12.viii.1978. *P. dictyodes:* 1a + 4s + 2 juv. s.

185. Near Thiem, 100 m, rainforest. Rainfall 2800 mm. L. Price coll. 15.x.1967. FMNH 159219. *P. dictyodes:* 1a.

TABLE 1 (Continued)

185. Near Thiem, 100 m, rainforest. Rainfall 2800 mm. L. Price coll. 15.x.1967. FMNH 159219. *P. dictyodes:* 1a.

186. N side of Tiwaka River, near Ouagap, 100 m, rainforest. Rainfall 3200 mm. L. Price coll. 11.x.1967. FMNH 159247. *P. dictyodes:* 3a + 1 juv. a.

187. S side of Amoa River, 4 km up the valley, 20 m, rainforest. Rainfall 2800 mm. A. Warén coll. 8.viii.1978. *P. dictyodes:* 3s + 2 juv. s.

188. N side of Tiwaka River, 13 km up the valley, 100 m, forest. Rainfall 2500 mm. P. Mordan, A. & S. Tillier coll. 17.i.1981. *P. dictyodes:* 7s + 1 juv. s + 2 broken.

189. E side Col des Roussettes, 400 m, rainforest. Rainfall 1700 mm. L. Price coll. FMNH 159325. *P. dictyodes:* 2a.

190. Col d'Amieu, 530 m, rainforest. Rainfall 1800 mm. L. Price coll. 1967. *P. dictyodes:* 10a + 2 juv. a.

191. Dothio-Nakey, 400 m, rainforest. Rainfall 2000 mm. L. Price coll. 21.x.1967. FMNH 159341. *P. dictyodes:* 2a.

192. Near Mt. Ouénarou, 200 m, rainforest. Rainfall 2300 mm. L. Price coll. 15.xi.1967. FMNH 159239. *P. dictyodes:* 3a. *P. mouensis:* 3a.

193. Forêt Cachée, 250 m, valley of the Creek Pernod, rainforest. Rainfall 2700 mm. McKee coll. 29.vi.1978. *P. dictyodes:* 1s.

194. Faux Bon Secours, 300 m, rainforest. Rainfall 3000 mm. McKee coll. 17.iii.1980. *P. dictyodes:* 1s.

195. 8 km S of Yaté, 30 m, rainforest. Rainfall 3000 mm. L. Price coll. 19.xi.1967. FMNH 159238 *P. marteli:* 10a + 7 juv. a.

Pararhytida was collected from forest with rainfall ranging from 1200 mm to more than 6000 mm a year. It is absent from very dry environments, and also from high-altitude rainforest ("forêts à mousses"). It appears that with the exception of *P. dictyodes*, which is found throughout the entire rainfall range of the genus, each species is restricted to a part of this range.

Living *Pararhytida* is always found at ground level, resting in the leaf litter. Dead and rotting palm sheaths are a particularly favoured resting site; the snails are never found associated with logs, a site occupied by a number of other New Caledonian charopid genera.

ANATOMY AND MORPHOLOGY

Shell

The shell of *Pararhytida* is very large for a charopid, ranging from 13.5 mm to 37 mm in diameter. No other endodontoid is known to reach such a large size (Solem, 1961; 1976; 1983). The shell is rather flat (H/D ranging from 0.44 to 0.65, with a mean of 0.56), and carinated. The umbilicus is open and rather small, from 0.055 to 0.15 (mean 0.088) the shell diameter. The adult shells have from 5.5 whorls in small species, to 6.9 whorls in the largest (*P. dictyodes*).

The aperture of adult shells is slightly expanded, but not deflected as in many endodontoids. As the shell takes on the adult characters (in its last 0.2 of a whorl), the position of maximum apertural height is displaced outwards from the columellar extremity of its basal border to the middle of the latter.

Shell sculpture consists of oblique radial ridges, which are too dense and faint to be accurately counted. The apical whorls of large *P. dictyodes* have only coarse radial ridges, whereas the apical whorls of smaller species additionally show traces of very faint spiral sculpturing (Fig. 2A). In New Caledonian charopids the distinction between groups having radial apical sculpture and those having spiral apical sculpture is much less well defined than was stated by Solem (1961).

The colour pattern consists primarily of reddish-brown flammules radiating outwards from the suture, on a light beige background. The flammules are generally well defined only near the suture; further away they are interrupted by pale zones and spotted by almost white, oval specks. Young shells of *P. mouensis* and *P. pyrosticta* are known to have periostracal hairs along the carina (Fig. 2B) which, as shown by Preston's original description of *Tropidotropis gudei*, resemble those of *Tropidotropis*.

Foot and pseudo-operculum

The foot of *Pararhytida* is aulacopod. Its most striking feature is the presence of a pseudo-operculum on the tail (Solem, Tillier & Mordan, 1984), formed from a dorsal epidermal thickening. It occupies the same position as the prosobranch operculum, and completely occludes the shell aperture when the foot is retracted. It is not horny as in prosobranchs. Surprisingly, neither Fischer (1875) nor Starmühlner (1970), both of whom dissected *P. dictyodes*, mentioned this feature. A similar structure is found in the New Caledonian charopid genus *Rhytidopsis*, but

FIG. 1. Map of collecting stations (listed in Table 1).

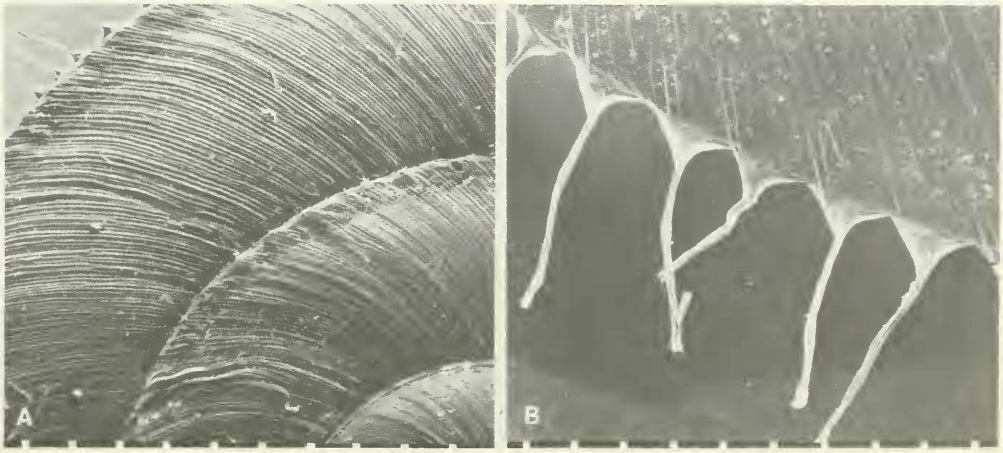


FIG. 2. Shell of juvenile *P. pyrosticta* n. sp., Tchingou, sta. 84. A. Surface sculpture, scale 300 μm. B. Carinal hairs, scale 100 μm.

TABLE 2. Number and size of radular teeth in *Pararhytida*.

Species	No. specs.	Number of teeth			Width of tooth in mm			
			Per side		Central		Lateral	
		Per row	Marg.	Lat.	Mesocone	Whole tooth	Mesocone	Whole tooth
dictyodes	11 (1 juv.)	79–93	23–30	14–19	12.5–22.5	20.5–38.5	15.5–28.0	23–45
mouensis	4	65–75	20–26	11–14	12–16.5	26–32.5	16.5–22	30–39
marteli	1	67	21	12	13	26.5	20.5	30
phacoides	2 (1 juv.)	69	24	10	12.5	26	13	30.5
pyrosticta	2	67–71	22–23	11–12	9.5–11	20–20.5	12–13.5	22.5–23
thyrophora	1	75	22	15	8.5	25	16	30

is known from no other stylommatophoran. The supposed function of the pseudo-operculum in efficiently blocking the shell aperture implies a novel pattern of foot retraction in the Stylommatophora: instead of being proximal to the mantle border inside the shell cavity when retracted, the tail of *Pararhytida* remains distal to the border. Furthermore, its tip has to be retracted before its dorsal side, such that only the pseudo-operculum remains exposed in the fully retracted animal.

Jaw and radula

The jaw is thin, arcuate and smooth. It is not very rigid and is easily dissolved by sodium hypochlorite solution. Its size appears to vary roughly in proportion to that of the animal.

The overall pattern of radular anatomy in *Pararhytida* is relatively uniform, and conforms well to the standard charopid pattern described by Solem (1983: 34). The central tooth is tricuspid, and smaller and narrower than the adjacent laterals. The lateral teeth are also tricuspid, but asymmetrical in that the endocone is often slightly higher than the ectocone, and typically rather narrower. The transition from laterals to marginals is gradual, occuring over two to three teeth, thus making precise counting of the numbers of laterals and marginals impossible. The marginal teeth are tricuspid and have a highly characteristic shape: the mesocone is normally broad and blunt; the endocone is of equal height to, or slightly shorter than the mesocone, and strongly falciform, pointing in towards the mesocone; the ectocone is sharp, conical, and with its tip normally well below the top of the tooth.

The anterior surfaces of the central and lateral teeth bear a characteristic group of shallow pits and grooves (Fig. 14) which presumably form part of the inter-row support mechanism (Solem, 1972), and articulate with the basal plate of the tooth in front. Table 2 lists the ranges of tooth number and size for the material examined. It is clear from the data for *P. dictyodes*, where a relatively large number of specimens have been examined, that there can be great intra-specific variation. Also, the table demonstrates that there is considerable size overlap between the various species. There were no obvious differences seen in the radulae of sympatric species pairs: *P. mouensis* and *P. marteli* from sta. 47 had remarkably similar radulae, in both tooth number and shape, and sympatric populations of *P. dictyodes* and *P. mouensis* (sta. 192) had normal radulae for their species. Indeed, the most extreme forms of *P. dictyodes* were found in allopatric situations. From the limited information available, there would thus appear to be no evidence for any form of character displacement in the radular morphology of *Pararhytida*.

Visceral mass

In *Pararhytida* the total length of the visceral mass varies from 3.5 to 5.5 whorls, but intraspecific variation never exceeds one whorl. Its length is not directly proportional to the length of the coiled shell since the species with the most whorls (*P. dictyodes*) has the shortest visceral mass (Table 3).

The length of the lung varies from 0.5 to 1.2

TABLE 3. Length in whorls of various parts of the visceral mass.

Sta.	Visc. mass	Lung	Top of stomach	Stomach	Upper spire
Pararhytida dictyodes					
7	3.6	0.75			
20	4	0.66	1		2.33
25	3.3	0.75	1		1.55
25	3.35	0.75	1.1	0.9	1.5
79	4.5	0.75	1.3	1(0.25)	2.4
80	5.25	0.8	1.25	1.1(0.25)	3.2
83	4	0.75	1		2.25
86	3.25	0.6	0.75	0.66	1.9
91	3.25	0.55	1.2	1	1.5
110	4.4	0.75	1.15	1	2.5
115	3.75	0.75	1.2	1(0.25)	1.9
118	4.25	0.6	1.15	1?(0.25)	2.5
123	4.2	0.7	1.2	1?(0.25)	2.3
184	3.6	0.75	1.3		1.55
185	3.5	0.75	1.3		1.45
186	3.45	0.8	0.9		1.75
189	3.75	0.5	1		2.25
190	3.75	0.75	1	0.75	2
191	?	0.75	1		?
192	4	0.8	1	?(0.3)	2.2
Pararhytida mouensis					
43		1.2	1.2		
47	5.2	0.95	1.25		3
128	4.5	0.95	1.1		2.55
136	4.3	1.15	1.1		2.05
141		1.1			
179	4.2	0.9	1.3		2
192	4	1	12		1.8
Pararhytida marteli					
47	5.4?	1.05	0.9		
48	5.6	1.3	1		3.3
48		1.2	1.1		
195	5.5?	0.9	1.1		3.5?
Pararhytida phacoides					
97	4.2	0.9	1.2		2.1
118		0.6(juv.)			
Pararhytida pyrosticta					
72	4.75	0.65	1.1	1(0.2)	3
84	4.9?	0.85	1.15		2.9
84	5.1?	0.75	1.15	1	3.2
91	4?	0.75	1.25		2?
Pararhytida thyrophora					
58	5.4?	0.6	1.4	1.3(0.2)	3.4?

whorls above the pallial border. Within a species, maximum variation is 0.4 whorls. The stomach and crop, which generally occupy an entire whorl, have their distal extremity normally between 0.9 and 1.2 whorls above the lung, although exceptionally it may lie further down (0.75 whorls in some *P. dictyodes*), or up (1.4 whorls in *P. thyrophora*). The upper part of the visceral mass, which includes the digestive gland and hermaphrodite gland, varies in length between 1.5 and 3.5 whorls, and almost as much variation may be found within a single species (Table 3).

Internally the digestive tract shows only faint oesophageal ridges, and no crop ridges or typhlosole.

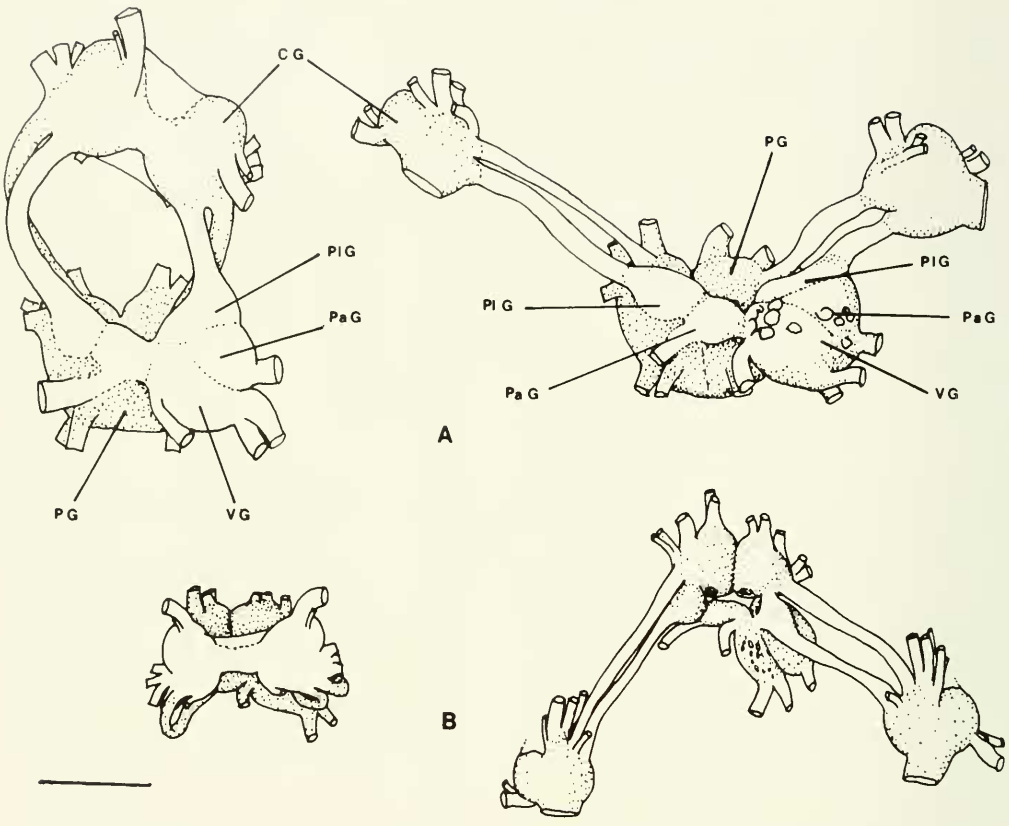


FIG. 3. Central nervous system of *Pararhytida*. A. *P. dictyodes*, Col d'Amos, sta. 66; B. *P. marteli*, S of Yaté, sta. 195. Scale line both 1 mm. CG, cerebral ganglion; PaG, parietal ganglion; PG, pedal ganglion; PIG, pleural ganglion; VG, visceral ganglion.

Central nervous system

The central nervous system has been described by Fischer (1875) and Starmühlner (1970), but with so little accuracy that no useful comparisons can be made. In particular, Fischer's figure misled Bargmann (1930) to erroneous conclusions concerning the pattern of compaction of the visceral chain: the visceral ganglion is not, in fact, fused with the left parietal ganglion. Within *Pararhytida*, the arrangement of the central nervous system seems to relate primarily to size:

1. In the four smallest species the cerebral commissure and the lateral connectives are relatively long (Fig. 3B). 2. In the large *P. dictyodes*, the cerebral commissure is short, and the lateral connectives shorter, particularly on the right side (Fig. 3A); the left parietal ganglion is attached to the left pleural ganglion, and the visceral, right parietal, and right pleural ganglia form a single mass in which individual ganglia are barely distinguishable. 3. In species of intermediate size (*P. mouensis*), the arrangement of the central nervous system is also intermediate.

In all species the ganglia of the visceral chain are adpressed, and displaced to the right to such an extent in small species that the left parietal ganglion is close to the median plane; in the large *P. dictyodes* it actually lies in the median plane. Additionally, in small species, the right parietal ganglion has moved to a position underneath the right pleural (Fig. 3A).

Pulmonary complex

The kidney is U-shaped (Fig. 4), and varies from almost one-half to a little less than

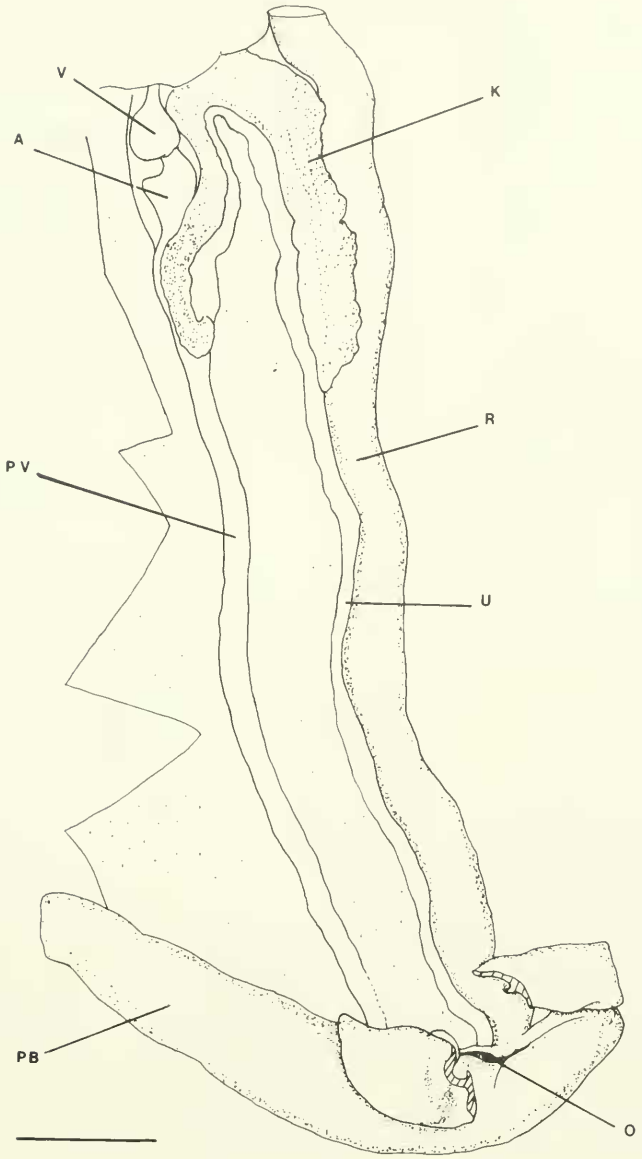


FIG. 4. Pallial complex of *Pararhytida dictyodes*, Le Cresson, sta. 5. Scale line 5 mm. A, auricle; K, kidney; O, anus and ureter opening; PB, pallial border; PV, pulmonary vein; R, rectum; U, ureter; V, ventricle.

one-third the length of the lung. The two arms of the kidney are subequal in *P. phacoides* and *P. pyrosticta*; the rectal arm is slightly longer than the cardiac arm in *P. thyrophora* and *P. dictyodes*, and is about 1.5 times the length of the cardiac arm in *P. mouensis* and *P. marteli*.

Only the principal pulmonary vein can be clearly distinguished on the lung roof, which does not have any other obvious venation. The rectum and ureter open contiguously on the dorsal side of the pneumostome, and the opening is protected ventrally by a small lappet of the mantle border.

FIG. 5. A, genital apparatus of *Pararhytida dictyodes*, showing position of spermatophore, Mt. Table Unio, sta. 110. B, spermatophore. Scale lines both 5 mm. AG, albumen gland; E, epiphallus; HD, hermaphrodite duct; HG, hermaphrodite gland; O, oviduct; P, penis; PA, penial appendix; PR, penial retractor; SO, spermoviduct; SP, spermatheca; Sp, spermatophore; T, talon; V, vagina; VD, vas deferens.

Genital apparatus

Hermaphrodite and female portion (Fig. 5A)

The hermaphrodite gland is composed of between three and seven lobes, and their number can vary considerably within a species (from three to six in *P. dictyodes*, and from four to seven in *P. mouensis*). The two extremities of the hermaphrodite duct are thin and almost straight, but the median portion is thickened and convoluted, forming a seminal vesicle (*sensu* Bayne, 1973). Its distal end opens into the stalk of a spherical talon, whose intraspecific variation in size may be as great as that within the entire genus (½ or slightly more).

The size of the albumen gland is also variable, apparently depending primarily on the degree of maturity. When fully developed, it occupies most of the space between the top of the kidney and the crop, as in most charopids (Solem, 1983). The length of the free oviduct varies from one-half to about twice the spermoviduct length. It is usually contorted, and maintained in this state by connective tissue attached to a branch of the retractor muscles, which inserts in the angle between the oviduct and spermathecal stalk. Its wall is thick and internally bears coarse, longitudinal ribs.

The spermatheca is always short, its top never reaching as far as the carrefour region. It is adpressed to the columellar side of the spermoviduct. The head varies from pear-shaped to elongate, and shape appears fairly constant within species. The spermathecal stalk is thick-walled, with longitudinal internal ribbing. Generally it contains a curious structure resembling a small, hard, hemispherical knob, housed in a horseshoe-shaped ridge (e.g. Fig. 19D). The position of this structure varies, even within species, from just above the oviducal opening to the top of the spermathecal stalk. Its function is unknown.

The vagina is long, and in all but one species contains a large, transverse ridge. *P. mouensis* has only a vaginal constriction which, from its position, may well be homologous with the ridge (Fig. 28B). This species additionally possesses one or two vaginal pouches or appendices close to the constriction. In all species the atrium is very short.

Penial complex (Fig. 5A)

This comprises a short, fusiform penis with a subapical (possibly glandular) appendix, and a long, thin epiphallus. The penis retractor muscle is inserted at the penis/epiphallus junction, and originates about one-fifth the way up the inner lung wall.

The internal ornamentation of the penis (Fig. 19) consists basically of two main longitudinal pilasters: one interrupted by the opening of the penial appendix, and often bifurcated at its upper part; the second situated on the opposite side, and extending further up the penis. The upper part of the second pilaster may be prominent, forming a kind of verge, and may also be prolonged as a transverse ridge running between the opening of the epiphallus and the opening of the penial appendix. The space between these two pilasters is often occupied by a number of less-prominent secondary pilasters. This pattern may be altered in various ways: all pilasters may be equally developed, or so reduced that only an apical verge may be distinguished within the penis. In some cases the epiphallic pore is prominent, or surrounded by a circular ridge, reminiscent of the ring pilaster of typical charopids (Solem, 1983). A few millimeters above the pore, the wall of the epiphallus bears numerous ridges; further up only three ridges are normally distinguishable, two of which are larger than the third. The junction of the epiphallus and vas deferens does not show any particular morphological differentiation, being marked only by the termination of the epiphallic ridges and by a diminution in the diameter of the duct.

Spermatophore (Fig. 5B)

Although previously undescribed in charopids, the occurrence of a horny spermatophore appears to be the rule rather than the exception in New Caledonian members of this family (Tillier, unpublished). In *Pararhytida* the spermatophore is always elongate-fusiform in shape and bears a longitudinal ridge. Complete spermatophores have only been recorded from within the spermatheca, when the spermatophore pore has been directed towards the oviduct. In some species it is prolonged by a long tail which runs down the spermathecal stalk and then up the free oviduct, reaching as far as the spermoviduct

(Figs. 5A, 27D, 37A). When such a tail is developed, the spermatophore ridge extends to its extremity, where it becomes finely denticulated. The function of this tail is most probably to transport the sperm from the spermathecal head to the spermoviduct.

TAXONOMIC CRITERIA

This section considers the rationale upon which the taxonomic decisions taken in this paper were made. The basic criterion used to decide whether two forms belong to different species was the absence of intermediate forms, which we suppose reflects the absence of gene flow. Two situations may arise: 1. The two forms are sympatric. In such a situation specific distinction has been easy as there is normally a large morphological gap between taxa. Such situations have allowed us to gauge the degree of interspecific character difference expected within the group. 2. The two forms are allopatric. If the morphological gap is smaller than that between sympatric (more strictly syntopic) species, then we have considered the forms conspecific. When the gap is larger, as has happened frequently, one can either separate the two forms as distinct species, or integrate them into a coherent pattern of intraspecific geographic variation.

An example will illustrate this last case. There are greater character differences between some northern and southern *P. dictyodes* than between sympatric *P. dictyodes* and *P. phacoides*. However, we have considered the former to be conspecific because in this case not only does each character vary along a geographical cline, but also the morphoclines themselves vary independently, and we have interpreted this as evidence of continuous gene flow. The alternative situation would be one in which there is congruence between morphoclinal discontinuities, suggesting areas where gene flow is absent or severely restricted.

Where any major doubt has remained, our decision has been to lump rather than split. Particularly in the cases of *P. dictyodes* and *P. mouensis*, however, we cannot exclude the possibility that our taxonomy has been too conservative; had there been less material of either species more taxa would probably have been recognised.

The result is that in *Pararhytida* no single character seems to allow species recognition throughout the genus: species are defined in terms of character combinations, in relation to geographical position. In all cases intrapopulation variation is much lower than that between allopatric populations; that is, variation is mainly geographic.

Multivariate analysis of clinal variation in both conchological and anatomical characters of *Pararhytida* will form the subject of a further paper.

SYSTEMATIC REVIEW

Genus *Pararhytida* Ancey, 1882

Type species: *Helix dictyodes* Pfeiffer, 1847 (by subsequent designation of Pilsbry, 1894: 52).

Diagnosis

Pararhytida differs from all known charopid genera, other than *Rhytidopsis*, by its pseudo-operculum and by the presence of a transverse ridge, sometimes developed into a foliated appendage, within the vagina. It differs from *Rhytidopsis* by: 1. Its mode of life in the leaf litter (*Rhytidopsis* is arboreal); 2. The simplicity of the transverse vaginal ridge, which is considerably more complex in *Rhytidopsis;* 3. The shape of the penis and the long, thin epiphallus; and 4. Its large, flattened carinated shell, and weak shell sculpture. (The anatomy and biology of *Rhytidopsis* will be the subject of a further paper.)

Micromphalia Ancey, 1882 and *Plesiopsis* Ancey, 1888 were considered by both Franc (1956) and Solem (1961) to be subgenera of *Pararhytida*. As they possess neither a pseudo-operculum nor any kind of peculiar vaginal structure, they are here removed from *Pararhytida*.

Pararhytida dictyodes (Pfeiffer, 1847) (Figs. 4–20)

Helix dictyodes Pfeiffer, 1847: 111 (New Guinea). Gassies, 1863: 241, pl. 1, fig. 19; Fischer, 1875: 273.

Helix dictyoides [sic] Pfeiffer. Reeve, 1852: pl. 80, species 423.

Trochomorpha dictyodes (Pfeiffer). Crosse, 1894: 241, pl. 8, fig. 3.

Pararhytida dictyodes (Pfeiffer). Dautzenberg, 1923: 140.
Pararhytida (Pararhytida) dictyodes (Pfeiffer). Franc, 1956: 136; Solem, 1961: 467; Starmühlner, 1970: 302, figs. 14-18.

Lectotype (here designated): New Guinea (in error), Lieutenant Ince, Cuming Collection. BMNH Reg. no. 1981262 (Fig. 6). Dimensions (mm): Shell height 16.1. Shell diameter 27.1. Aperture height 10.6. Aperture diameter 13.9. Umbilicus width 2.8. Whorls 6.25.

Paralectotypes: 2 specimens from above lot. BMNH Reg. no. 1981263. Dimensions (mm): Shell heights 14.5, 15.2. Shell diameters 26.2, 26.8. Aperture heights 10.0, 10.5. Aperture diameters 13.3, 13.8. Umbilicus widths 2.4, 2.5. Whorls 6.4, 6.1.

Other material: Sta. 7(2), sta. 9(2), sta. 12(7), sta. 14(2), sta. 16(5), sta. 18(5), sta. 19(3), sta. 20(9), sta. 25(19), sta. 36(1), sta. 37(1), sta. 65(5), sta. 66(29), sta. 69(1), sta. 70(4), sta. 71(16), sta. 74(1), sta. 79(5), sta. 80(7), sta. 83(20), sta. 86(2), sta. 88(1), sta. 89(2), 91(8), sta. 94(11), sta. 97(2), sta. 98(13), sta. 110(5), sta. 114(5), sta. 115(2), sta. 116(4), sta. 117(2), sta. 118(9), sta. 119(2), sta. 123(4), sta. 131(10), sta. 142(2), sta. 143(2), sta. 146(1), sta. 181(4), sta. 183(14), sta. 184(7), sta. 185(1), sta. 186(4), sta. 187(5), sta. 188(10), sta. 189(2), sta. 190(12), sta. 191(2), sta. 192(3), 193(1), sta. 194(1).

Preserved material: 5, 6, 7, 12, 16, 20, 25, 65, 66, 71, 79, 80, 83, 86, 91, 98, 110, 114, 115, 116, 118, 119, 123, 131, 146, 181, 183, 184, 185, 186, 189, 190, 191, 192.

Distribution

P. dictyodes occurs principally on the mainland; it is absent from the Belep Islands, and its presence on the Isle of Pines (Crosse, 1894) has not been confirmed by recent collections. It appears to be absent from the coastal areas along the W coast, and also from the extreme SE. It is, however, the most widely distributed species of *Pararhytida*, tolerating the greatest range of altitude and rainfall (Table 1).

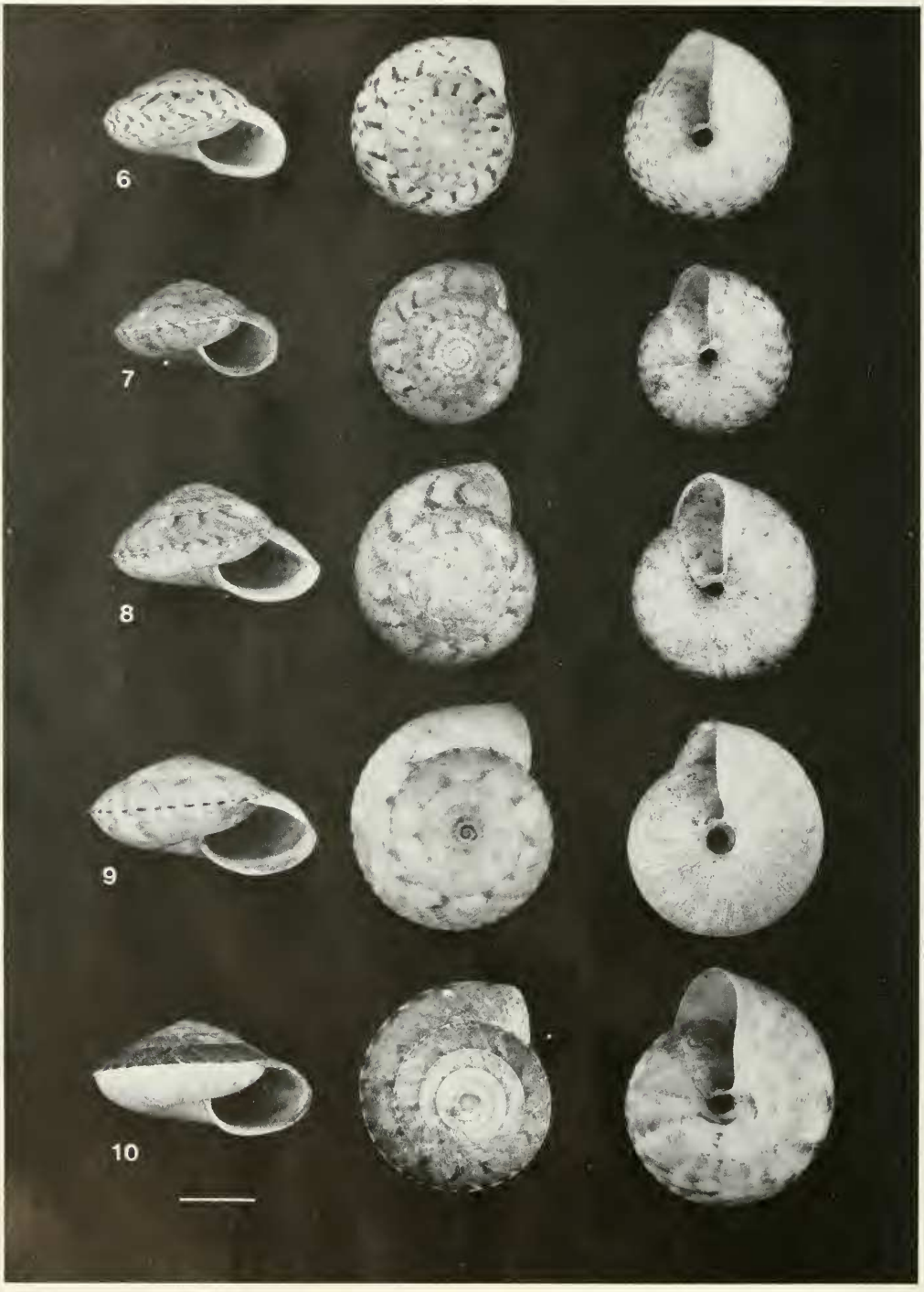
Shell

The shell of *P. dictyodes* is generally larger than in other species, ranging from 21 × 11.1 mm to 36.8 × 21.2 mm. There are from 5.6 to 6.9 whorls (mean 6.24, s.d. 0.19) in adult shells. Its dimensions overlap only with those of *P. mouensis* from the extreme SE (Mt. Guemba, sta. 47), where *P. dictyodes* does not occur. The only shell character allowing constant specific recognition, even in juveniles, is the relative flatness of the shell apex.

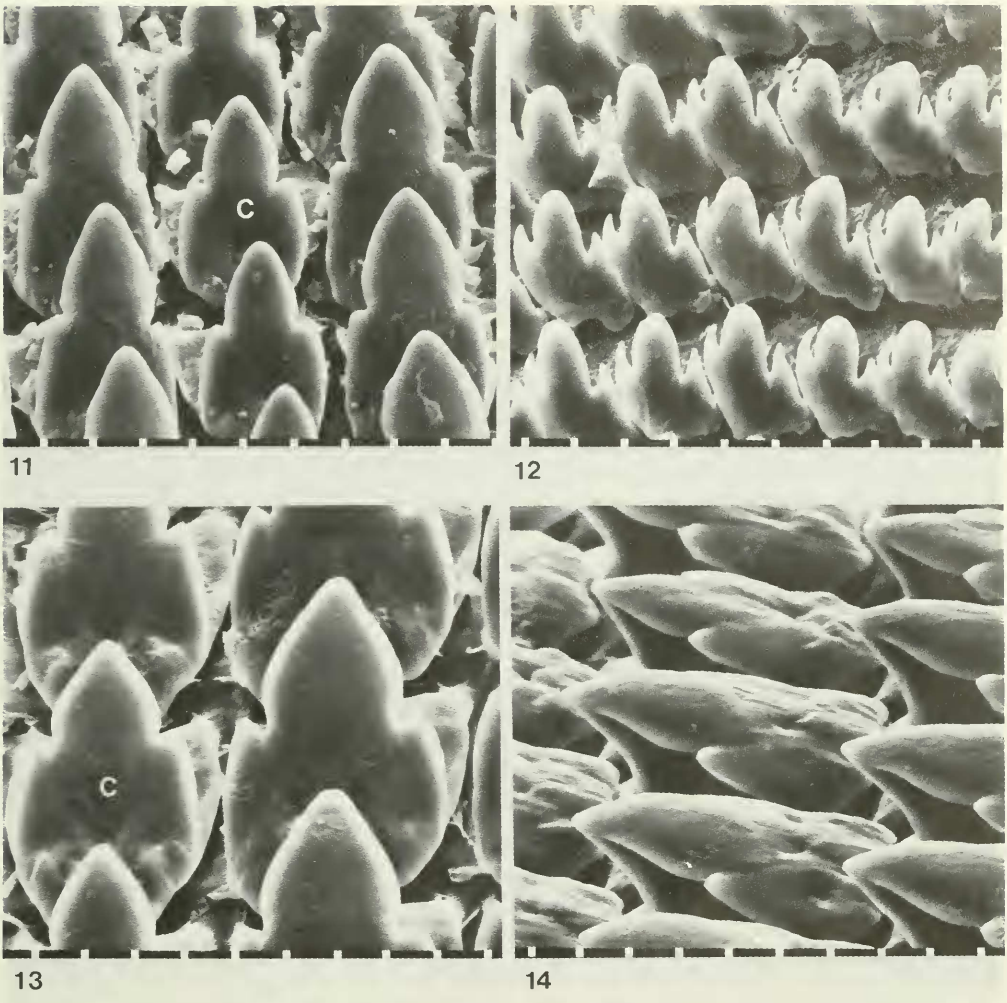
Geographic variation in shell dimensions is considerable and will form the subject of a further paper. The shell is relatively small in the extreme N (Fig. 7), and in some localities on the NW side of the mainland (Mt. Koniambo, sta. 88; Plateau de Tango, sta. 16). Its size increases southeastwards, and approaching the isolated massifs along the northwestern coast (eastern coast: stas. 83 (Fig. 8), 86, 89, 185, 186, 187, 188; northwestern massifs: 12, 20, 97). The maximum size is reached SE of the Houailou valley (around stas. 110, 114 (Fig. 9), 189). In the SE plains (stas. 142, 192, 193, 194 (Fig. 10)) size again decreases slightly.

Radula (Figs. 11–14)

One juvenile and eleven adult radulae, from a wide geographical range of sites, were examined with a stereoscan electron microscope. The species shows considerable variation in tooth size, overlapping at the lower end of the range with the five other species (Table 2). The number of teeth per row, however, always exceeded that of other *Pararhytida* species. Overall tooth shape varies particularly in respect of the central tooth, which appeared to be especially narrow at stations on the NE coast (stas. 66, 80, 184); Fig. 11 shows the normal central and lateral dentition of *P. dictyodes*. There was little difference between the central and lateral teeth of immature and adult individuals at sta. 91, although the marginals of the former were markedly narrower (Fig. 12). A radula with quite exceptionally large teeth (Figs. 13, 14) was recorded from Mt. Paeoua, but other similarly isolated mountain sites nearby (stas. 91, 189) did not show any tendency towards size increase. Specimens of *P. dictyodes* occurring sympatrically with *P. pyrosticta* (sta. 91), *P. phacoides* (sta. 118), and *P. mouensis* (sta. 192) all appear to have quite normally sized teeth, and in the last case (sta. 192) the two co-occurring species have radular teeth of almost identical size.



FIGS. 6–10. 6. *Helix dictyodes* Pfeiffer, lectotype, BMNH 1981262. New Guinea [*sic*], leg. Lieutenant Ince, Cuming Collection. 7. *P. dictyodes*, Grottes de Koumac, sta. 6. 8. *P. dictyodes*, Thiem, sta. 83. 9. *P. dictyodes*, Rembai, sta. 114. 10. *P. dictyodes*, Faux Bon Secours, sta. 194. Scale line all 10 mm.



FIGS. 11–14. 11. Central and lateral teeth, *P. dictyodes*, Tiwaka, sta. 186. 12. Marginal teeth, *P. dictyodes*, Aoupinié, sta. 91. 13. Central and lateral teeth, *P. dictyodes*, Mt. Paéoua, sta. 20. 14. Side view of lateral teeth, *P. dictyodes*, Mt. Paéoua, sta. 20. Scale divisions all 10 μm.

Pulmonary complex

The length of the lung (Fig. 4) is normally about 0.75 whorls. It never exceeds 0.8 whorls, and is shorter (0.5–0.6 whorls) in the wet stations between the valleys of the Amoa and Houailou rivers (stas. 86, 91, 189). The rectal arm of the kidney is slightly longer than the cardiac arm, and its length is ca. ⅓ the lung length.

Genital apparatus (Figs. 5, 15–20)

As with the shell and other organ systems, the genital apparatus of *P. dictyodes* shows considerable geographic variation. However, each part of the genital system shows independent clinal variation.

Hermaphrodite gland (Figs. 5, 15–18): In the northern part of the mainland (stas. 5, 7, 65, 66, 71, 79, 80, 183, 184; Figs. 15A, B, C)

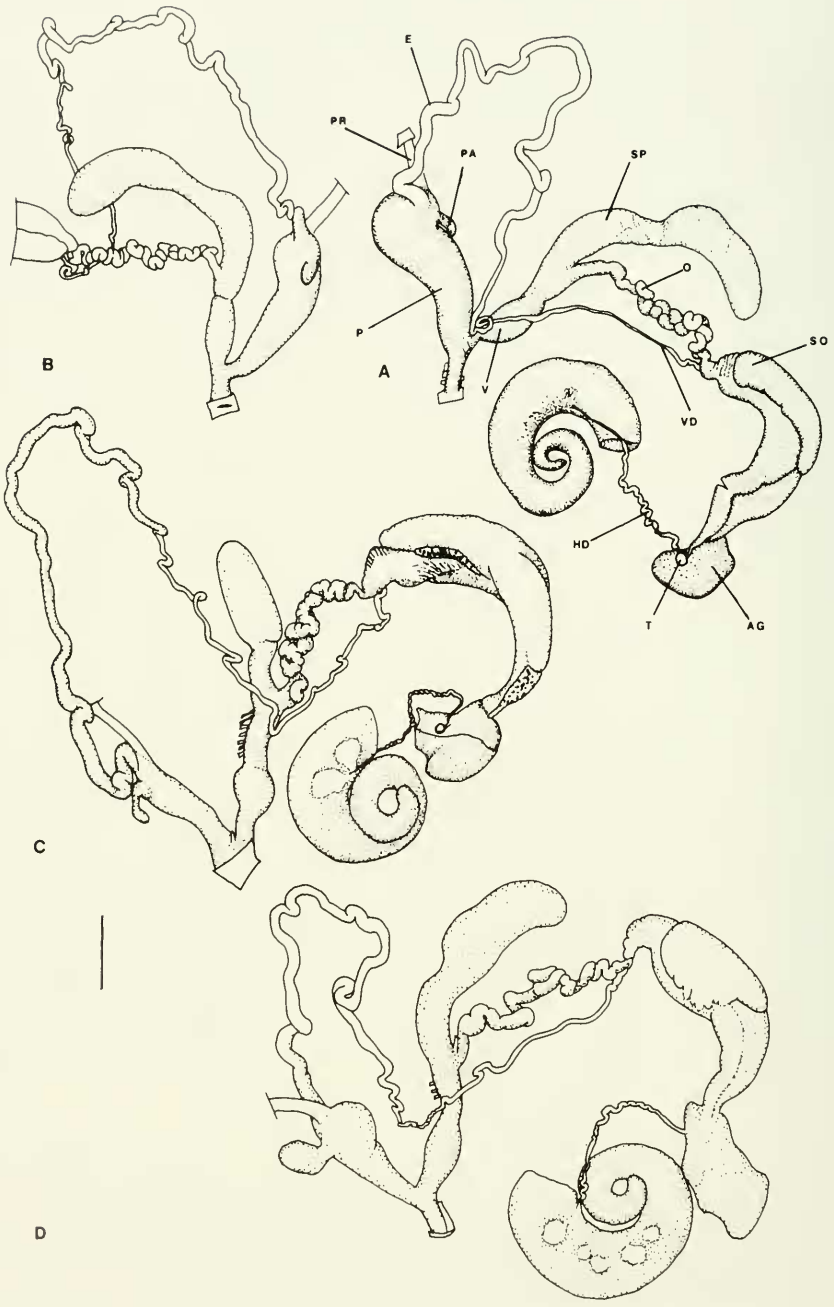


FIG. 15. Genital apparatus of *Pararhytida dictyodes*. A, sta. 5; B. sta. 184; C. sta. 80; D. sta. 83. Scale line all 5 mm. AG, albumen gland; E, epiphallus; HD, hermaphrodite duct; HG, hermaphrodite gland; O, oviduct; P, penis; PA, penial appendix; PR, penial retractor; SO, spermoviduct; SP, spermatheca; T, talon; V, vagina; VD, vas deferens.

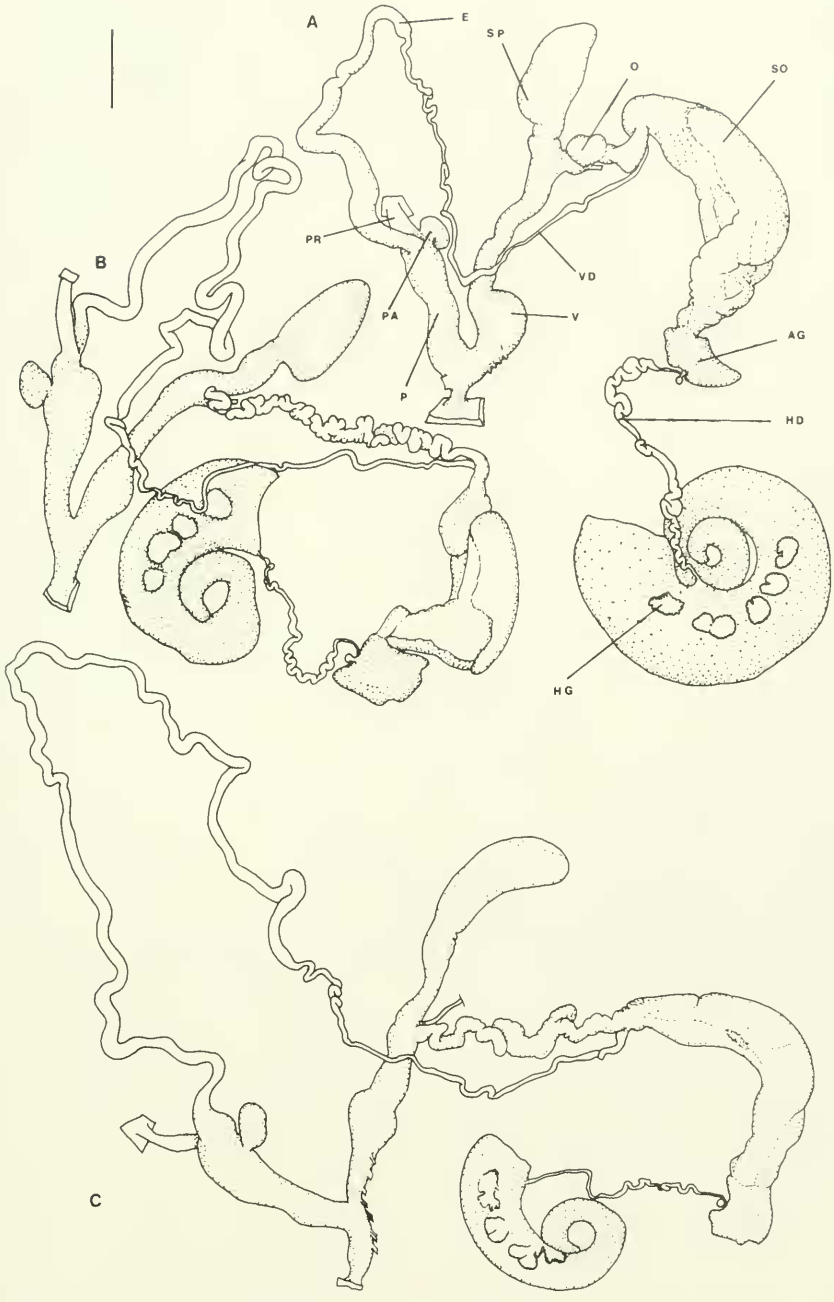


FIG. 16. Genital apparatus of *Pararhytida dictyodes*. A, sta. 20; B. sta. 91; C. sta. 25. Scale line all 5 mm. AG, albumen gland; E, epiphallus; HD, hermaphrodite duct; HG, hermaphrodite gland; O, oviduct; P, penis; PA, penial appendix; PR, penial retractor; SO, spermoviduct; SP, spermatheca; V, vagina; VD, vas deferens.

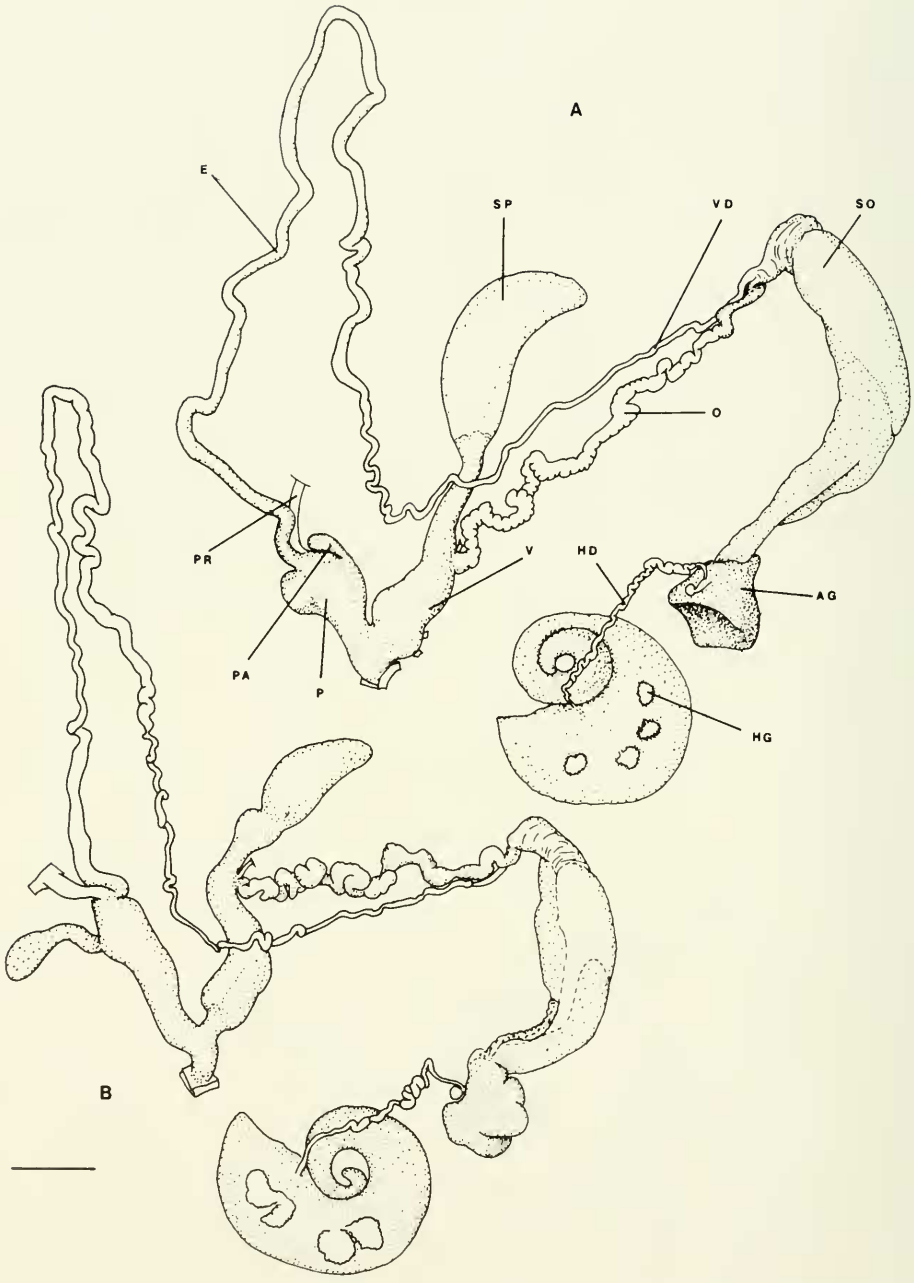


FIG. 17. Genital apparatus of *Pararhytida dictyodes*. A, sta. 115; B. sta. 189. Scale line both 5 mm. AG, albumen gland; E, epiphallus; HD, hermaphrodite duct; HG, hermaphrodite gland; O, oviduct; P, penis; PA, penial appendix; PR, penial retractor; SO, spermoviduct; SP, spermatheca; V, vagina; VD, vas deferens.

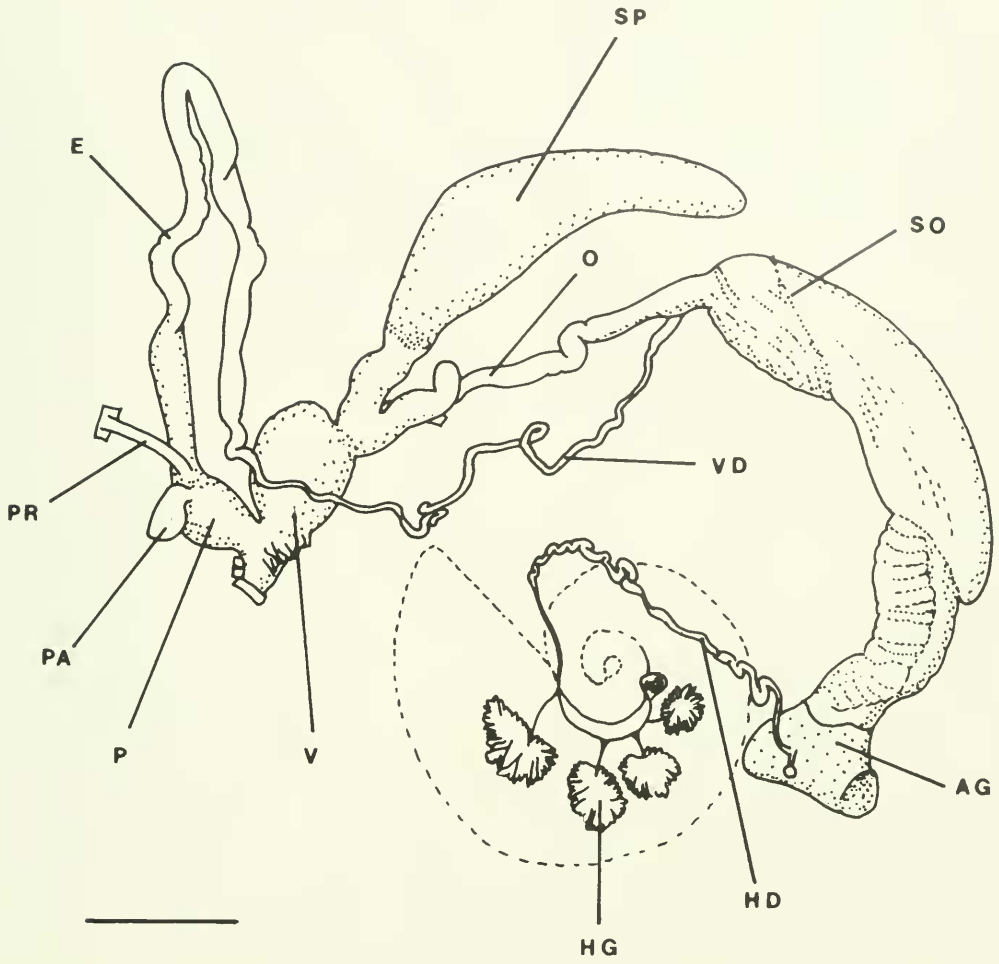


FIG. 18. Genital apparatus of *Pararhytida dictyodes*, sta. 192. Scale line 5 mm. AG, albumen gland; E, epiphallus; HD, hermaphrodite duct; HG, hermaphrodite gland; O, oviduct; P, penis; PA, penial appendix; PR, penial retractor; SO, spermoviduct; SP, spermatheca; V, vagina; VD, vas deferens.

it comprises five lobes, but along the E coast there is a progressive tendency for the second and third lobes (that is, from the top of the stomach) to fuse: at Thiem (sta. 83, Fig. 15D) they are almost fused and further southeastwards (stas. 25, 86, 91, 185, 186; Figs. 16 B, C) fusion is complete. In the central western massif of the Paéoua (sta. 20) the hermaphrodite gland has five (or possibly six) lobes; this may simply be an effect of increased size (the snails are larger than at sta. 25, the nearest from which we have preserved material), or it may be that the number of lobes remains constantly five along the NW coast (there is no preserved material between stas. 6 and 20). Further southeastwards, between the Col des Roussettes, the Col d'Amieu, and Mt. Do, the number of lobes is reduced to three by the fusion of the upper two lobes (stas. 110, 123, 189, 190; Fig. 17B), but eastwards and southwards it becomes four again (stas. 115, 118, 191, 192; Figs. 17A, 18).

Albumen gland and spermoviduct: size variation in the albumen gland, talon and spermoviduct was not analysed because this appears to depend principally on the state of maturity of the animal.

Free oviduct: generally this is longer than the spermatheca when uncoiled; when coiled it is compacted along the spermatheca stalk. It does, however, show enormous geographical variation in length, by up to about four times. It tends to be shorter in the NE valleys (stas. 86, 185, 186), and reaches its minimum on the central Mt. Paéoua (sta. 20, Fig. 16A). It seems that the reduction in length of the free oviduct from N to S is gradual, whereas the increase in length southeastwards is rather abrupt between stas. 20 (Fig. 16A) and 86 on the one hand (short oviduct) and sta. 91 on the other (long oviduct). The oviducal length is intermediate at sta. 25 (Fig. 16C). In the S plains (sta. 192, Fig. 18) the oviduct is again shorter than further N.

Spermatheca and vagina: the head of the spermatheca is thin-walled and smooth. It is always elongate, and almost constant in shape. Its size is more or less uniform within each of two large geographical regions: it is smaller north of the Col d'Amieu (sta. 190; circa 1 cm in length), and larger S and E of this station (circa 1.5 cm in length). In the S plains (sta. 192) it is again reduced to about the same size as S of the Col d'Amieu.

The spermathecal stalk and vagina form a single functional unit, as shown by the absence of any discontinuity in internal ornamentation at the level of oviduct insertion (Figs. 19, 20). The total length of this unit is almost constant over the entire range of the species, being shorter only in the S plains (sta. 192, Fig. 20D), but the relative size of stalk and vagina exhibit considerable geographic variation. The stalk is longer than the vagina in the NW region (stas. 65, 66, 70, 71, 184), and shorter on the E slope of Mt. Panié (stas. 79, 80). The stalk continues to reduce in relative length southeastwards (stas. 83, 185, 186), reaching a minimum at stas. 20 and 86. Its relative length again increases southeastwards of these stations, and from the Col d'Amieu southeastwards the stalk length is equal to or slightly greater than that of the vagina.

The level of insertion of the transverse vaginal ridge is generally at the mid-point of the length of the vagina, but varies between the lower quarter at Mt. Paéoua (sta. 20, Fig. 20A) and the upper extremity of the vagina at Mt. Ouénarou (sta. 192, Fig. 20D). This variation in the position of the ridge is probably also geographic, since it lies below the middle of the vagina in all stations around Mt. Paéoua (stas. 25, 86, 91, 115, 189, 190; Figs. 20B, C), that is, in central New Caledonia.

The transverse ridge in the vagina is never perfectly symmetrical, tending to be more expanded on the penial side (Fig. 19A). In Thiem (sta. 83), on Mt. Paéoua (sta. 20, Fig. 20A) and in the southern Mt. Ouénarou (sta. 192, Fig. 20D), this trend is developed to a point where the transverse ridge becomes a foliated appendage hanging in the vagina, attached only along a small portion of the vaginal circumference. Along the NW coast at least, this particular character-state is developed along a cline: an intermediate condition can be observed in stations along the northwestern coast around Thiem (stas. 80, 86, 184, 185; Figs. 19 B, C).

The position of the knob inside the spermathecal stalk varies independently from the length of the latter: in N populations (southwards to stas. 20 and 86), it is at about the same level or just above the oviducal opening; from stas. 25 and 91 southeastwards it is at the upper extremity of the stalk (Figs. 19, 20).

Penial complex: externally, the general trend is reduction in absolute and relative length of the penis proper from N (Fig. 15) to S (Fig. 18). In N New Caledonia, the eastern slope of Mt. Panié excepted, the penis is longer than the vagina (stas. 5, 7, 65, 66, 71, 183, 184; Figs. 15A, B). Further S the penis is generally slightly shorter than the vagina (Fig. 16). On the eastern slope of Mt. Panié (stas. 79, 80; Fig. 15C), in the Amoa and Tiwaka valleys (stas. 86, 186), and on Mt. Paéoua (sta. 20; Fig. 16A), the penis becomes much shorter than the vagina, although this is due more to a relative increase in the length of the vagina than to a shortening of the penis. From stas. 91 and 189 southeastwards the absolute length of the penis regularly decreases in correlation with the vaginal length (Fig. 17B). Penial shape also varies in relation to internal characters. In N stations (stas. 79 and 80 excepted) the two principal pilasters are particularly prominent, and the longer one apically inflated, even forming a verge in stas. 65, 66 and 183 (Fig. 19A). Correlatively the head of the penis becomes inflated (stas. 5, 7, 65, 66, 71, 83, 183, 184, 185; Fig. 15A, B, D). Further S, and on Mt. Panié, the apical part of the principal pilaster is weaker or even lacking and the two pilasters less prominent, resulting in a more fusiform penis (stas. 20, 25, 79, 80, 86, 91, 110, 186, 189; Figs. 15C and 19B,

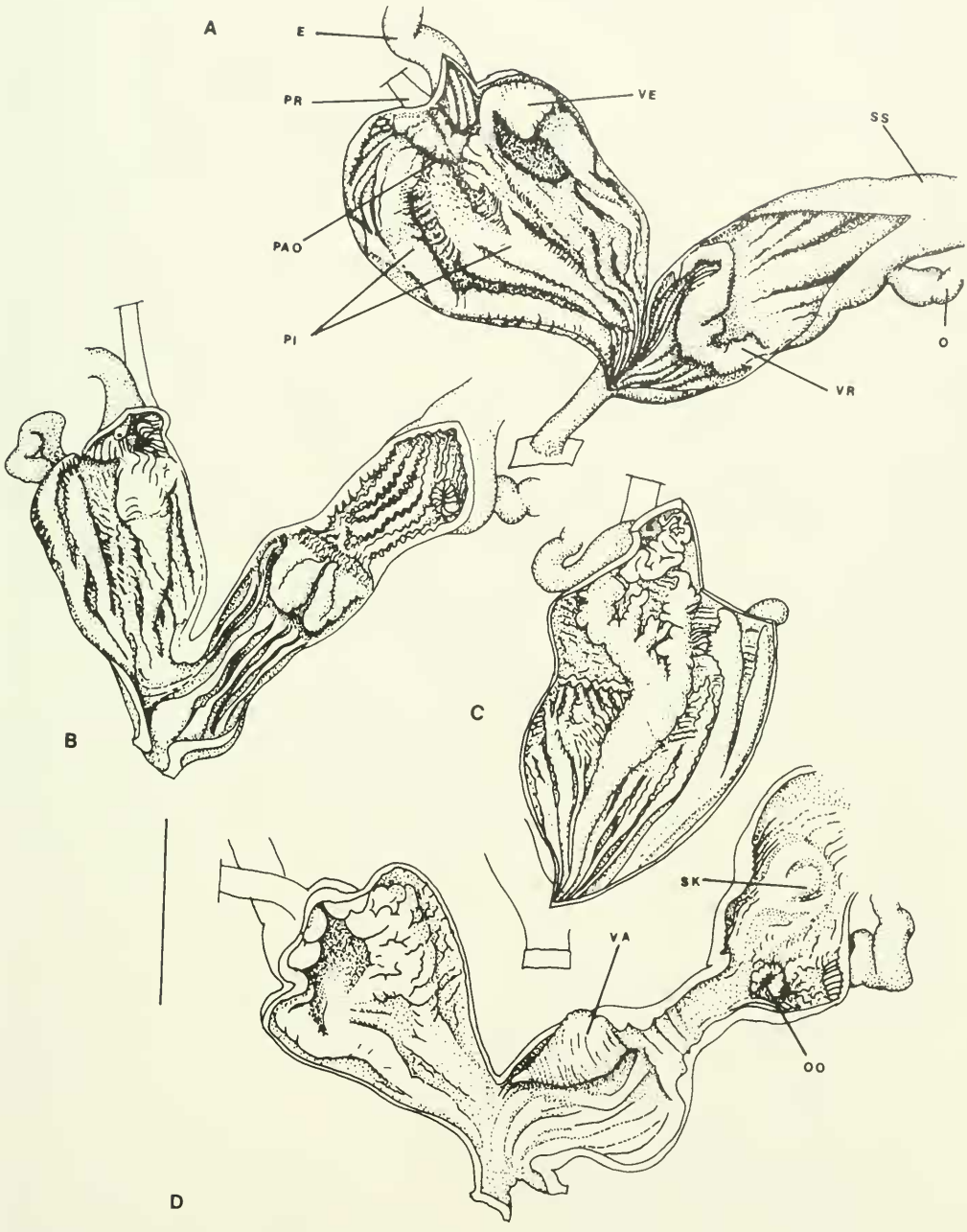


FIG. 19. Genital apparatus of *Pararhytida dictyodes.* A, sta. 66; B, sta. 80; C, sta. 184, D, sta. 83. Scale lines all 5 mm. E, epiphallus; O, oviduct; OO, oviducal opening; PAO, penial appendix opening; PI, penial pilasters; PR, penial retractor; SK, spermathecal knob; SS, spermathecal stalk; VA, vaginal appendix; VE, verge; VR, vaginal ridge.

FIG. 20. Genital apparatus of *Pararhytida dictyodes*. A, sta. 20; B, sta. 91; C, sta. 191; D, sta. 192. Scale lines all 5 mm. E, epiphallus; O, oviduct; OO, oviducal opening; PAO, penial appendix opening; PI, penial pilasters; PR, penial retractor; SK, spermathecal knob (cut in 20A); SS, spermathecal stalk; VA, vaginal appendage; VR, vaginal ridge.

16A and 20A, 6B and 20B). S and E of Col d'Amieu (stas. 115, 118, 123, 190, 191; Fig. 20C) the pilasters are thicker, stouter, and more regular. The longer principal pilaster is prolonged transversely between the opening of the penial appendix and the epiphallic pore, and one of the secondary pilasters is apically inflated. This internal morphology produces a penis which externally resembles that from the N stations, but which results from a different internal pilaster structure (Figs. 19A, 20C). In the southernmost station (192) the penis has only numerous more-or-less equal pilasters that abut apically onto a large transverse ridge (Fig. 20D).

Spermatophore: In contrast to most other genital characters, the size and shape of the spermatophore of *P. dictyodes* seems remarkably constant. It is horny, and comprises a fusiform body, and a thin tail at least five times the body length. The distal part of the tail is thicker than the proximal part (Fig. 5B), becoming thinner again towards its extremity, which is perforated. It bears a denticulate ridge which originates on the distal part of the spermatophore body.

Discussion

P. dictyodes is easily recognised by its large size and flat apical whorls. Anatomically, it is the only *Pararhytida* with: 1. A lung never exceeding 0.8 whorls in length, and typically shorter. 2. A spermathecal head of the size and shape described above. Other characters are so variable that they cannot be considered diagnostic.

The problem lies not so much in the recognition of *P. dictyodes* as defined here, but rather to be sure that all the populations studied belong to a single species. However, even if geographic forms could be recognised, the fact that characters appear to vary independently suggests that gene flow is indeed taking place.

Pararhytida mouensis (Crosse, 1868)
(Figs. 21, 24, 25, 27–29)

Helix mouensis Crosse, 1868: 152, pl. 8, fig. 5 (Mt. Mou).
Helix dictyonina Euthyme, 1885: 257 (Noumea).
Helix dictyonina var. *globulosa* Euthyme, 1885: 256.
Trochomorpha dictyonina (Euthyme). Crosse, 1894: 243, pl. 8, fig. 4; Dautzenberg, 1906: 258, pl. 8, figs. 4–6.
Pararhytida dictyonina (Euthyme). Dautzenberg, 1923: 140.
Charopa (Tropidotropis) gudei Preston, 1907: 220, fig. 7 (New Caledonia).
Pararhytida (Pararhytida) mouensis (Crosse). Franc, 1956: 137; Solem, 1961: 467.
Pararhytida (Pararhytida) dictyonina (Euthyme). Franc, 1956: 137; Solem, 1961: 467.

Lectotype of *H. mouensis* Crosse: MNHN. Mont Mou, Marie Colln. (Fig. 21). Dimensions (mm): Shell height 8.6. Shell diameter 17.3. Aperture height 6.4. Aperture diameter 8.2. Umbilicus width 2.7. Whorls 5.2.

Other type material: Lectotype (BMNH Reg. no. 1907.5.20.106) and paralectotype (BMNH Reg. no. 1923.2.20.7) of *C. gudei* Preston, New Caledonia, ex Preston. Lectotype and 5 paralectotypes (MNHN) of *H. dictyonina* Euthyme, New Caledonia (Fig. 22).

Other material: sta. 37(1), sta. 43(7), sta. 47(1), sta. 125(1), sta. 128(1), sta. 130(1), 136(4), sta. 140(1), sta. 142(7), sta. 150(1), sta. 179(6), sta. 192(3).

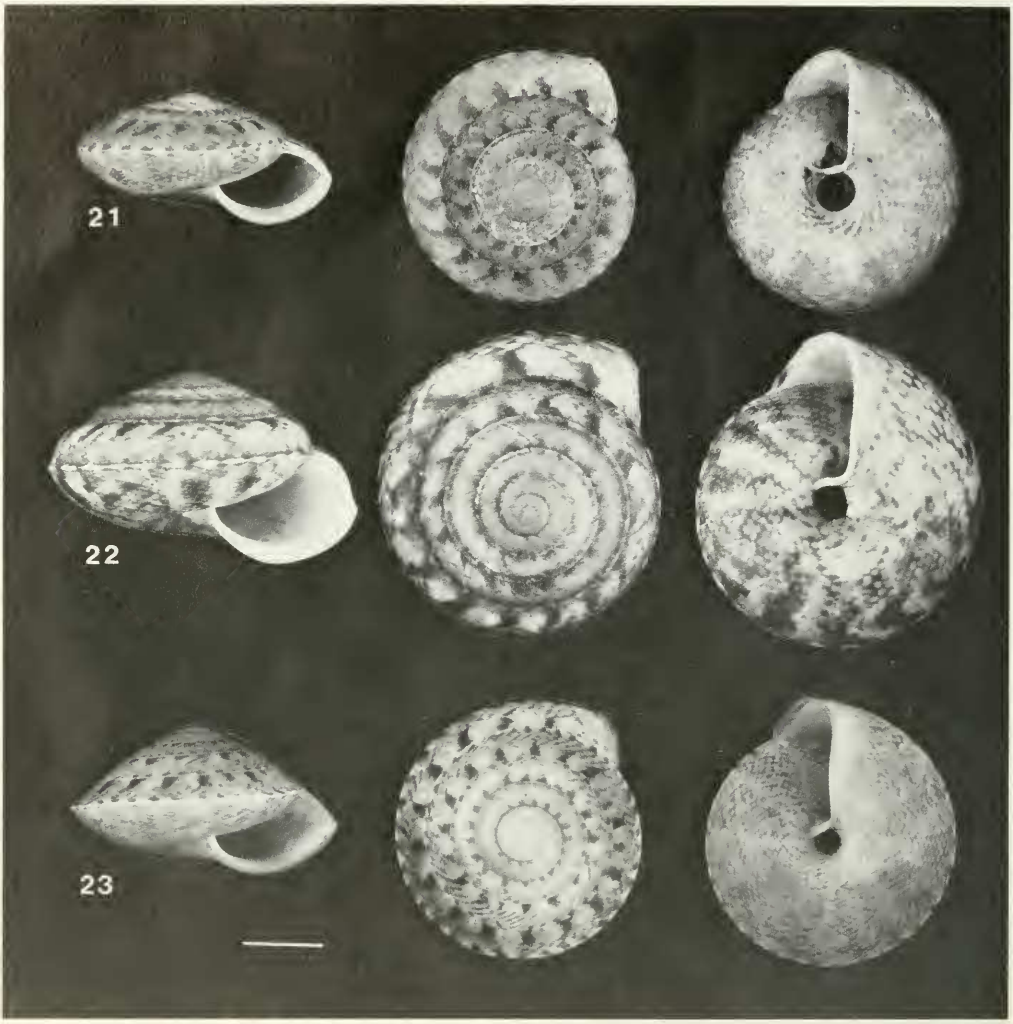
Preserved material: 37, 43, 47, 125, 128, 136, 140, 142, 179, 192.

Distribution

P. mouensis is restricted to the SE mainland of New Caledonia, from Mt. Humboldt (sta. 125) southeastward. We did not collect it in the coastal lowlands NW of Noumea, nor between Yaté and Goro (stas. 48, 49, 50, 195). It was found at stations with rainfall ranging from 1800 mm (Col de Mouirange, sta. 142) to 4500 mm (Mt. Humboldt, sta. 125). It occurs sympatrically with *P. dictyodes* at low altitudes in the S plains (stas. 142 and 192), and with *P. marteli* on Mt. Guemba (sta. 47).

Shell (Figs. 21, 22)

The shell varies in size from 18.9 mm × 10.5 mm to 24.9 mm × 15.1 mm. These extremes are found only at the edges of the range, the smallest in the W Mt. Koghi (sta. 140) and Mt. Mou (the type locality), and the largest on the eastern Mt. Guemba (sta. 47). The species is generally intermediate in size between the larger *P. dictyodes* and the remaining four smaller species. In contrast to *P. dictyodes*, the suture is moderately im-



FIGS. 21–23. 21. *Helix mouensis* Crosse, lectotype, MNHN. Mt. Mou, leg. Marie, 1868. 22. *Helix dictyonina* Euthyme, lectotype, MNHN. Noumea, Jousseaume Collection. 23. *Trochomorpha (Videna) marteli* Dautzenberg, lectotype, MNHN. New Caledonia. Scale line all 5 mm.

pressed. The shell is dome-shaped, quite unlike that of any other *Pararhytida*. The adult whorl count is broadly related to shell diameter, from 5.6 whorls in Mt. Koghi (sta. 140, D = 18.9 mm) to 6.25 whorls in Mt. Guemba (sta. 47, D = 24.9 mm) and 6.4 in Col de Mouirange (sta. 142, D ca. 22 mm); mean whorl count is 6.08 (s.d. 0.26).

Radula (Figs. 24, 25)

The radulae of four specimens were examined. The size and shape of individual central and lateral teeth are close to those of *P. dictyodes*, although appearing slightly shorter and broader, and show a considerable degree of variation (Table 2). The marginal teeth are in general shorter and narrower than in *P. dictyodes*, and both these and the laterals are typically fewer. At two of the four sites *P. mouensis* is sympatric with other species: with *P. marteli* at sta. 47, and with *P. dictyodes* at sta. 192. However there was as much radular variation between the two sympatric sites as between allopatric situations, and at sta. 47 tooth size and number

were almost identical in *P. marteli* and *P. mouensis*.

Pulmonary complex

The pulmonary cavity occupies the last 0.9 to 1.2 whorls of the visceral coil, but we did not have enough preserved material to distinguish any clear geographic pattern of variation. The rectal arm of the kidney is only slightly longer than the cardiac arm in northern stations (near Mt. Dzumac, sta. 128), but about 1.5 times longer in the southern plains (stas. 43, 47, 142, 179, 192).

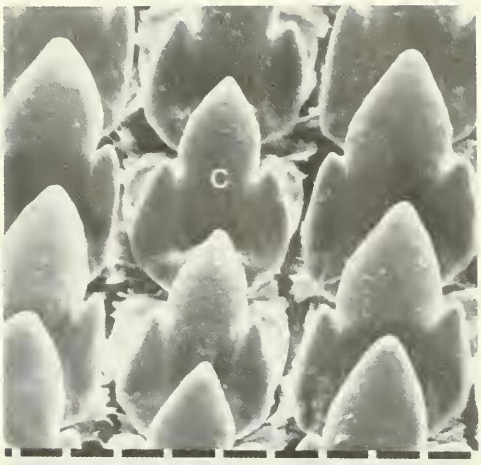
Genital apparatus

The number of lobes in the hermaphrodite gland increases from N to S, from four close to Mt. Dzumac (sta. 128), to five on the Montagne des Sources (sta. 136) and Mt. Ouénarou (sta. 192), six in the Rivière Bleue valley (sta. 43) and Mt. Guemba (sta. 47), and finally seven in the Col de Mouirange (sta. 142) (Fig. 27).

The relative length of the free oviduct also increases from N to S: it is shorter than the spermathecal length in northern stations (stas. 43 and 128; Figs. 27A, B), about the same length at station 136, and distinctly shorter at the other stations (sta. 47, 142, 179, 192; Figs. 27C, D).

The spermatheca has a highly characteristic shape, with a very long head of a constant diameter that is greater than the diameter of the short spermathecal stalk (Fig. 27).

The vagina does not possess a well-developed transverse ridge or internal appendage as do all other species (Fig. 28), but at most shows a thickening of the wall and an interruption in its longitudinal internal ridges. From their position, these ridges are considered homologous with those of other species; when present they are located below the mid-point of the vagina, except at sta. 128 (Fig. 28A). Although an internal ridge is lacking, the vagina of *P. mouensis* does possess one or two outgrowths of the vaginal wall which form pouch-like structures. These are not visible externally except as a thicken-



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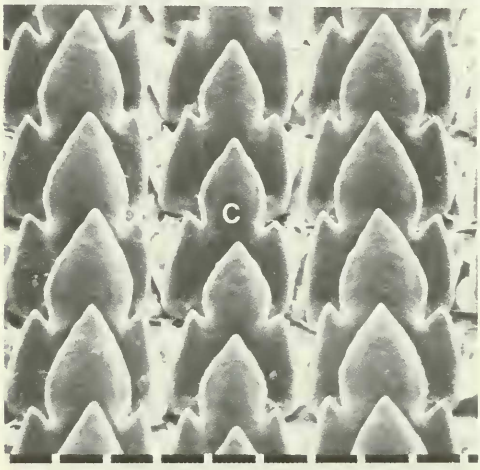

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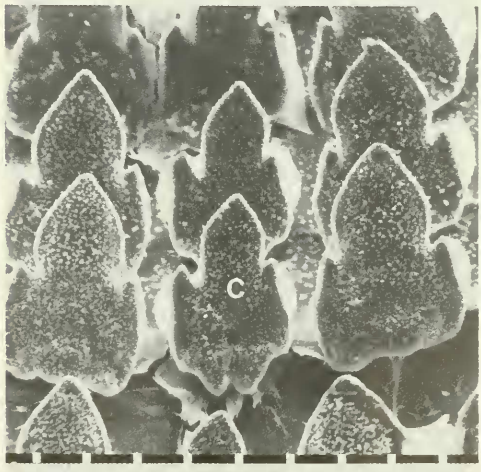

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FIGS. 24–26. 24. Central and lateral teeth, *P. mouensis*, Mt. Ouénarou, sta. 192. 25. Central and lateral teeth, *P. mouensis*, Col de la Ouinné, sta. 128. 26. Central and lateral teeth, *P. marteli*, Mt. Guemba, sta. 47. Scale divisions all 10 μm.

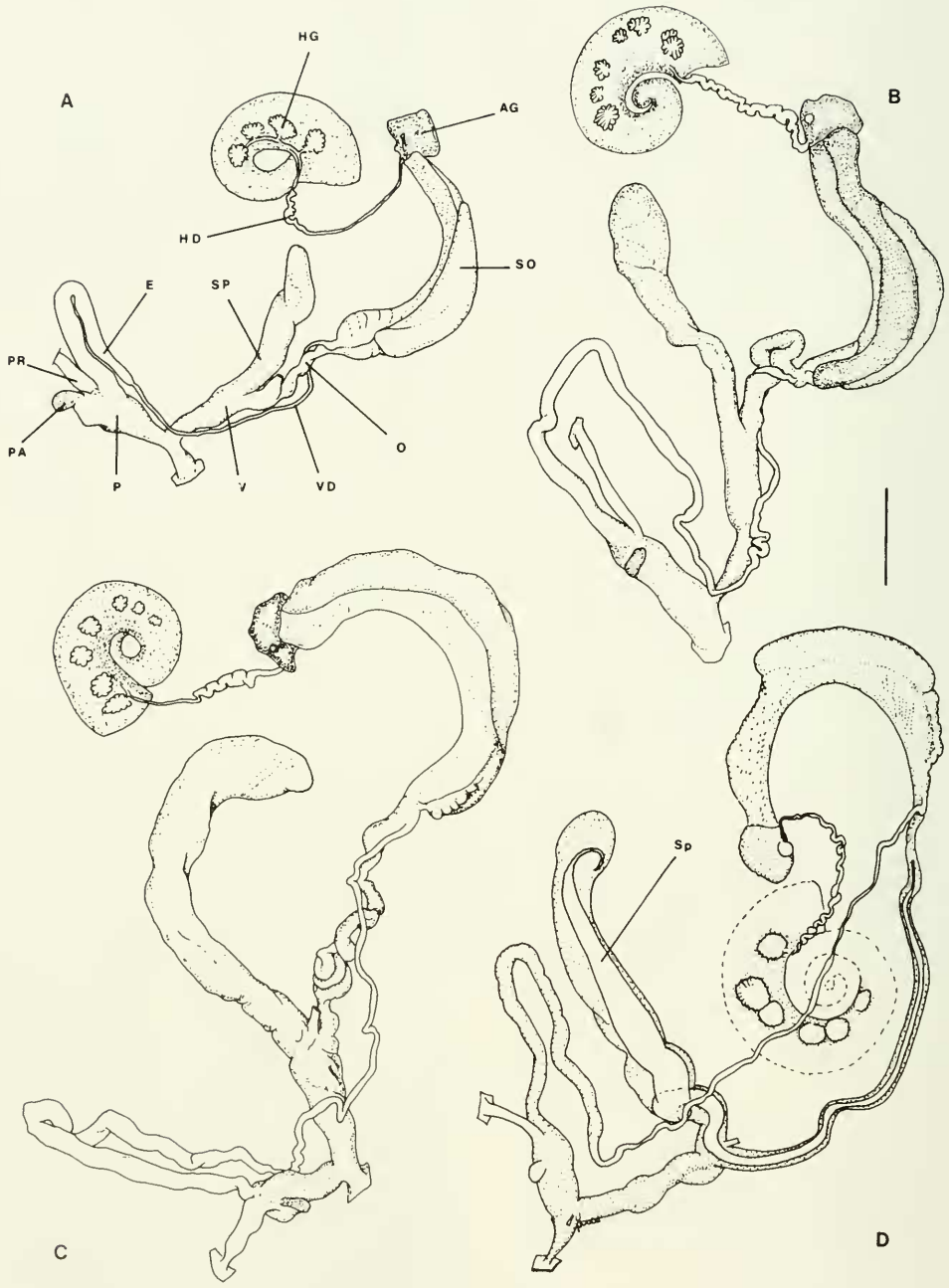


FIG. 27. Genital apparatus of *Pararhytida mouensis*. A, sta. 128. B, sta. 43. C, sta. 142. D, sta. 47, showing position of spermatophore. Scale line all 5 mm. AG, albumen gland; E, epiphallus; HD, hermaphrodite duct; HG, hermaphrodite gland; O, oviduct; P, penis; PA, penial appendix; PR, penial retractor; SO, spermoviduct; SP, spermatheca; Sp, spermatophore; V, vagina; VD, vas deferens.

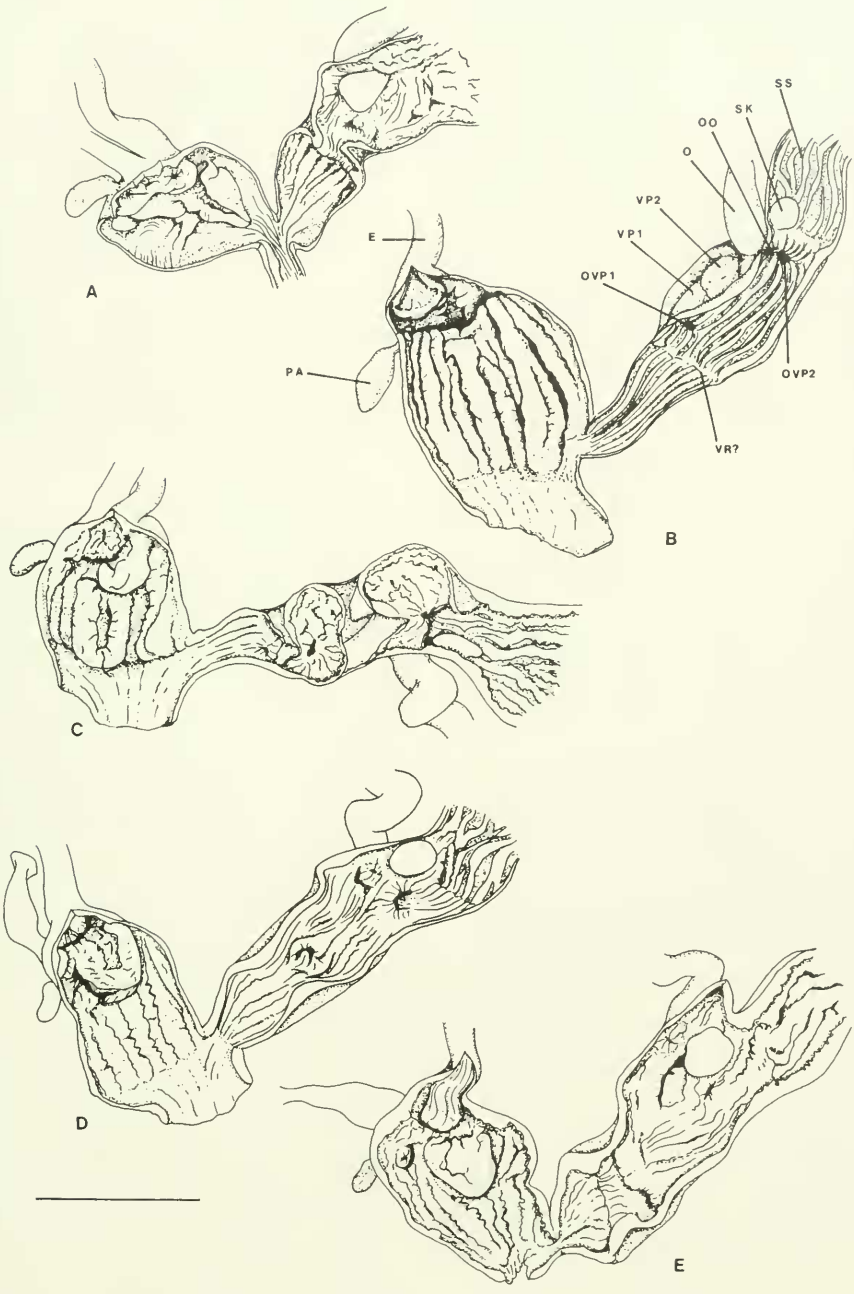


FIG. 28. Internal genital morphology of *Pararhytida mouensis.* A, sta. 128. B, sta. 43. C, sta. 48, showing the interior of the two vaginal pouches, but the vagina unopened within the sheath that surrounds the pouches. D, sta. 136. E, sta. 142. Scale lines all 5 mm. E, epiphallus; O, oviduct; OO, oviducal opening; OVP1, OVP2, openings of the vaginal pouches; PA, penial appendix; SK, spermathecal knob; SS, spermathecal stalk; VP1, VP2, vaginal pouches; VR, vaginal ridge.

ing of the vagina, being tightly bound in connective tissue, but are clearly visible when the vagina is opened (Figs. 28B, C). Their number and position vary geographically. In southern and central stations (stas. 43, 136, 179; Fig. 28B) the lower pouch lies just above the transverse ridge, and the upper pouch just beside the oviducal opening. In the NE (Mt. Guemba, sta. 47) only the upper pouch is present; this pattern probably arose through the loss of the lower pouch, which is less well developed in sta. 179 than in stas. 43 and 136. In the N (sta. 128, Fig. 28B) there is also a single upper vaginal pouch, but here it probably results from the fusion of the two pouches, since at the intermediate stations (142, 192) the two pouches are contiguous beside the oviducal opening (Fig. 28E). The knob in the spermathecal stalk is always situated just above the oviducal opening.

The penis is nearly constant in size, and is of a regular fusiform shape (Fig. 27). The epiphallus is a little more than twice as long as the penis, except in the northernmost station (128) where it is shorter (Fig. 27A). The internal ornamentation is typically formed of numerous short pilasters, and a verge originating from the upper end of the pilaster zone (Figs. 28A, C–E). This pattern may be modified, even within a population, by loss of the verge or weakening of the pilasters, the latter arrangement (Fig. 28B) permitting recognition of the homology of pilasters and verge between *P. mouensis* and *P. dictyodes*.

Spermatophore: these or fragments were only found at three stations (47, 136, 142); here the shape is fusiform, with no clear delimitation between body and tail (Fig. 29). A ridge runs the entire length of the spermatophore, appearing smooth at low magnifications, but minutely serrate at high. At Mt. Guemba (sta. 47), the spermatophore is much larger and more elongate than at the other stations. The size is probably related to the larger size of the animals there, but the change in shape is more problematic. At sta. 47 a spermatophore was found *in situ*, with its body in the spermathecal head, and the tail lying within the free oviduct (Fig. 27D).

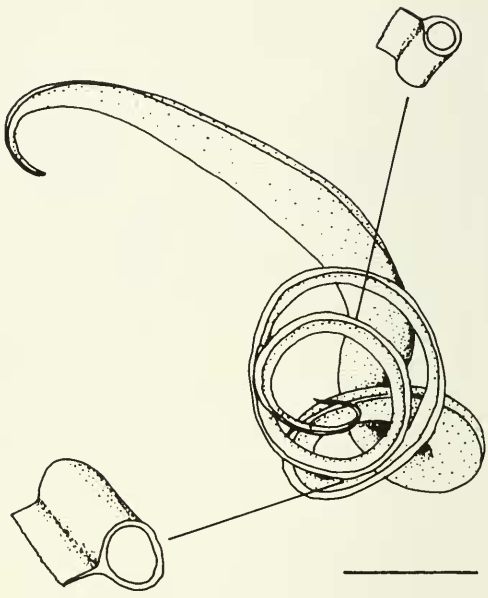


FIG. 29. Spermatophore of *Pararhytida mouensis*, sta. 47. Scale line 1 mm.

Discussion

P. mouensis is generally smaller than *P. dictyodes* and larger than the other four species of *Pararhytida*. It overlaps in size with *P. dictyodes* only at Mt. Guemba (sta. 47) where *dictyodes* has not been recorded, and with the other four species in the chain of Mt. Mou and Mt. Koghi (type locality and sta. 140), where similarly none of the small species is found. Conchologically it can be distinguished from *P. dictyodes* by its more impressed suture (especially on the first whorl), and from the small species by its rounded profile. It is the only species without a vaginal ridge or appendage, and possessing vaginal pouches. Although we were unable to collect topotypic material of *P. mouensis*, we are in little doubt that it is only the westernmost form of what has previously been called *P. dictyonina*, from which it differs in whorl number but not in rate of whorl increase. Furthermore, the shells of *P. dictyonina* become flatter at stations approaching those where typical *P. mouensis* occurs. The attribution of animals from Mt. Guemba to *P. mouensis* is more questionable, since their shells more closely resemble those of *P. dictyodes*. However, these animals are closer in anatomy to *P. mouensis* than to any other species, and we have no reason to preclude the possibility of a cline existing between Mt. Guemba and the remaining stations. Moreover, it seems

unlikely that the observed differences in spermatophore morphology between Mt. Guemba specimens and other *P. mouensis* are sufficient to prevent successful copulation. The anatomical change may result from sympatry with the smaller *P. marteli* at Mt. Guemba, and with the larger *P. dictyodes* over the rest of its range.

Pararhytida marteli (Dautzenberg, 1906)
(Figs. 23, 26, 30)

Trochomorpha (Videna) marteli Dautzenberg, 1906: 257, pl. 8, figs. 7–9 (New Caledonia).
Pararhytida (Pararhytida) marteli (Dautzenberg). Franc, 1956: 138; Solem, 1961: 467.

Lectotype (here designated): New Caledonia, leg. Martel, MNHN. (Fig. 23). Dimensions (mm): Shell height 9.8. Shell diameter 17.9. Aperture height 6.8. Aperture diameter 8.7. Umbilicus width 1.7. Whorls 5.9.

Other material: sta. 47(1), sta. 48(36), sta. 49(20), sta. 50(1), sta. 195(17).

Preserved material: 47, 48, 49, 50, 195.

Distribution

P. marteli has been recorded only from the extreme SE of New Caledonia, from Yaté (close to sta. 47) to Goro (sta. 50). However, we did not collect it from the Kouakoué, NW of sta. 47, and cannot be sure that it does not occur there. It was typically collected from stations with high rainfall, from 1900 mm to 3000 mm a year.

Shell (Fig. 23)

The shell is sharply carinated, domed above and shallowly rounded below, ranging in size from 16.1 × 8.8 mm to 20 × 10.9 mm. The carina is situated about half way up the palatal wall. Adult shells have from 5.2 to 6.2 whorls (mean 5.59; s.d. 0.2).

Radula

Only one radula was examined, from a specimen collected at Mt. Guemba (sta. 47, Fig. 26). The teeth are generally similar in shape, size, and number to *P. phacoides* (Table 2), and also to *P. mouensis* with which it is sympatric at sta. 47, although in the former case the lateral mesocones of *P. phacoides* are significantly smaller.

Pulmonary complex

The length of the lung varies between 0.9 and 1.3 whorls, as in *P. mouensis* (the stomach and crop have the usual length of one whorl, but the upper part of the visceral coil is longer than usual, extending between 3.3 and 3.6 whorls). The rectal arm of the kidney is about 1.5 times longer than the cardiac arm, and occupies less than 1/3 of the lung length.

Genital apparatus

The hermaphrodite gland has five lobes at stas. 47, 49 and 195 (Figs. 30A, C), but only four at Touaourou (sta. 48). Externally the genitalia resemble, in reduced form, those of *P. mouensis* (Figs. 27, 30). From N (sta. 47) to S (sta. 48 southward) the relative length of the free oviduct varies from slightly longer than the spermatheca to about half the length of the latter. Internally the only constant differences from the arrangement found in *P. mouensis* are the presence of a vaginal appendage and the absence of a vaginal pouch in *P. marteli*; the appendage is attached at the mid-point of the vagina (Figs. 30C, D).

Spermatophore: One complete spermatophore was found at Mt. Guemba (sta. 47; Fig. 30E). It has no tail and is smaller and stouter than in *P. mouensis*. Its longitudinal ridge is denticulate only at the open end.

Discussion

The shell of *P. mouensis* is thicker and more rounded than that of *P. marteli*. Although the anatomical differences between these two species are slight, their distinctness is confirmed at Mt. Guemba where they occur sympatrically.

Distinguishing the shells from those of *P. phacoides*, *P. pyrosticta* and *P. thyrophora* is more difficult: those of *P. marteli* are intermediate in shape between the more rounded *P. thyrophora* and the flatter *P. phacoides* and *P. pyrosticta*. In these last two species, the carina is situated higher on the whorl contour,

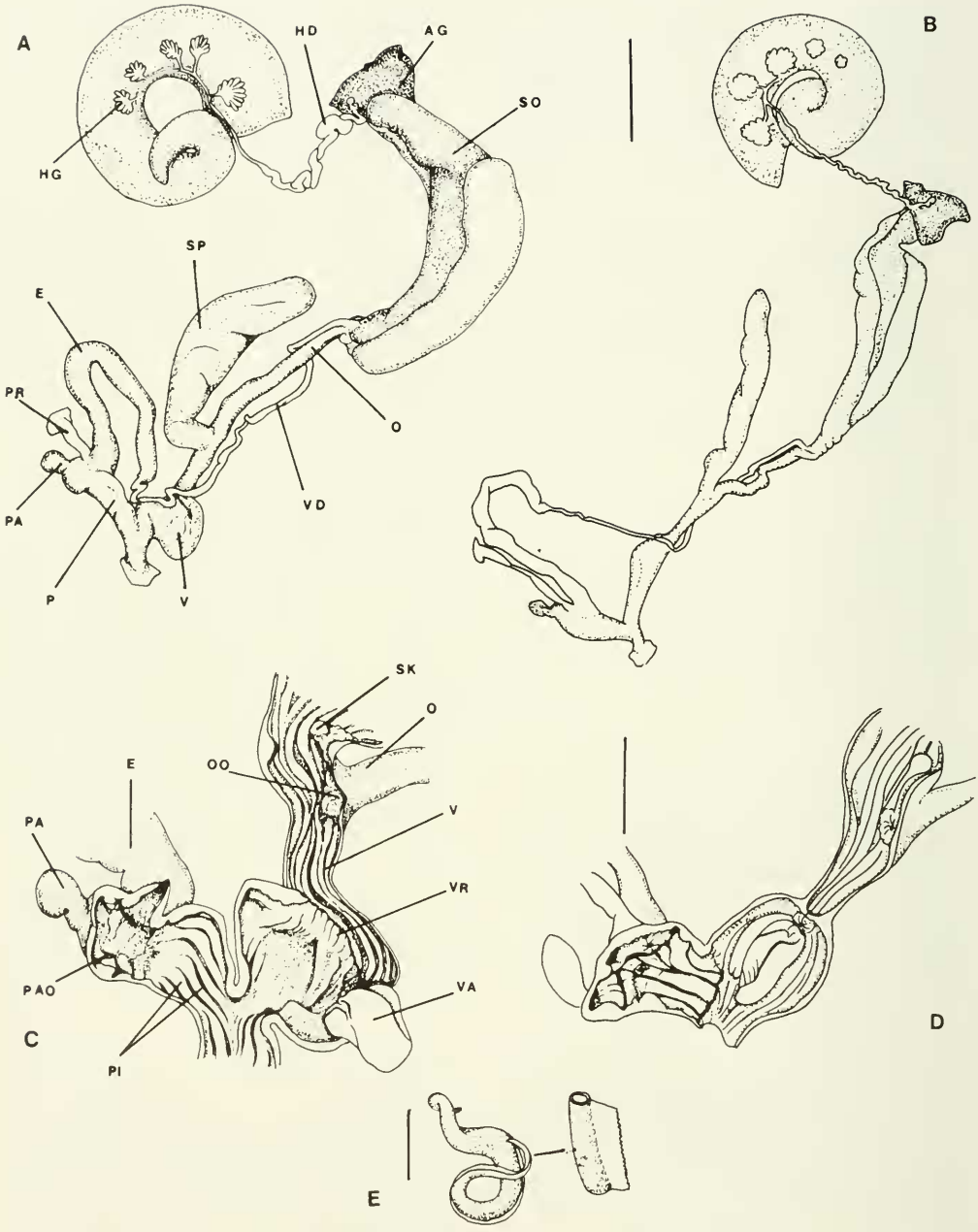


FIG. 30. Genital apparatus of *Pararhytida marteli*. A and C, sta. 195. B, External morphology, sta. 49. D, internal morphology, sta. 48. E, spermatophore, sta. 47. Scale lines A and B both 5 mm. C–E both 2.5 mm. AG, albumen gland; E, epiphallus; HD, hermaphrodite duct; HG, hermaphrodite gland; O, oviduct; OO, oviducal opening; P, penis; PA, penial appendix; PAO, penial appendix opening; PI, penial pilasters; PR, penial retractor; SK, spermathecal knob; SO, spermoviduct; SP, spermatheca; V, vagina; VA, vaginal appendage; VD, vas deferens; VR, vaginal ridge.

and they more closely resemble juveniles of *P. dictyodes*.

Pararhytida phacoides Mordan & Tillier, n. sp.
(Figs. 31, 34, 37)

Holotype: Mt. Boulinda, 980–1020 m, between Petit and Grand Boulinda, altitude rainforest. Coll. A. & S. Tillier, 6.vii.1979 (sta. 97), MNHN (Fig. 31). Dimensions (mm): Shell height 10.1. Shell diameter 19.4. Aperture height 7.3. Aperture diameter 9.9. Umbilicus width 1.7. Whorls 5.6.

Paratypes (preserved): 2, as above, MNHN.

Other material (preserved): sta. 118 (2 + 1 shell), 97 (1 broken shell).

Etymology: lens-like. Greek: phacos, a lentil.

Distribution

The two stations where this species was collected (stas. 97 and 118) probably represent the N and S limits of its distribution: to the N it is replaced by *P. pyrosticta* and to the S by *P. mouensis*. At both stations rainfall is high (3000 mm at sta. 97 and 2600 mm at sta. 118), and the distributions of the small *Pararhytida* species suggest that this relationship is not chance. *P. phacoides* is probably endemic to very wet rainforests on the mountains of southern central New Caledonia.

Shell (Fig. 31)

Only three adult shells were collected, ranging from 19.7 to 21.5 mm in width, from 9.7 to 10.6 mm in height, with an umbilicus of *circa* 2 mm in diameter. They have from 5.3 to 5.7 (mean 5.5, s.d. 0.18) whorls, and are sharply carinated, with the carina on the upper part of the palatal wall. The aperture is only slightly expanded. The upper surface of the initial whorls is convex, giving the shells a slightly more conical shape than in juvenile *P. dictyodes*. The border of the umbilicus of shells from Mt. Nakada is slightly shouldered.

Radula

Two specimens were examined from the only known localities for this species (stas. 97 and 118); the radula from sta. 118 was juvenile and was not measured. The radula from sta. 97 (Fig. 34) is similar to that of *P. marteli*, except that the marginal teeth tended to be broader, whilst the centrals and laterals are slightly narrower and more pointed.

Pulmonary complex

The lung occupies the final 0.9 whorl in the fully adult preserved specimen (sta. 97). The arms of the kidney are almost equal in length, which is about ⅓ of the total lung length. The pulmonary complex of *P. phacoides* is closer in anatomy to that of *P. dictyodes* than to either *P. mouensis* or *P. marteli*.

Genital apparatus

In both internal and external anatomy, the genitalia of *P. phacoides* resemble a reduced version of the genital apparatus of *P. dictyodes* (Figs. 37A, B). The hermaphrodite gland of the only specimen in which it was observed had four lobes. The only significant difference is in the shape of the spermathecal head, which is triangular and relatively shorter than in *P. dictyodes*. However, this shape may simply have been due to the presence of a spermatophore.

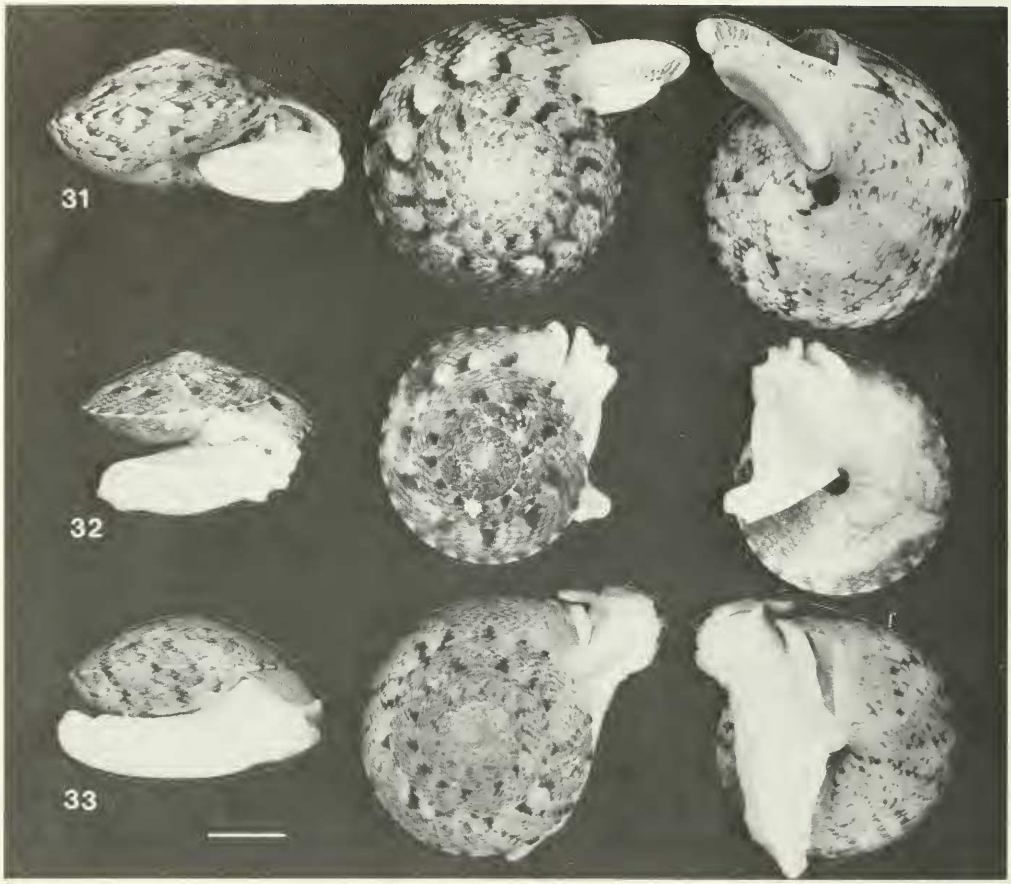
Spermatophore: this found at Mt. Boulinda is identical in shape and arrangement with those of *P. dictyodes*, and is only slightly smaller (Fig. 37C).

Discussion

If *P. phacoides* had not been found sympatrically with *P. dictyodes* at both stations where it was collected, separation from the latter would have been extremely difficult. It resembles closely a young *P. dictyodes*. There is, however, a slight difference in convexity of the early whorls, and also in rate of whorl increase, and maturity is reached at less than six whorls. In shell characters *P. phacoides* is simlar to *P. pyrosticta*, but the latter is slightly smaller for the same whorl count. Anatomical differences between *P. phacoides*, *P. pyrosticta* and *P. thyrophora* will be considered later.

Pararhytida pyrosticta Mordan & Tillier, n. sp.
(Figs. 2, 32, 35, 38)

Pararhytida marteli (Dautzenberg). Dautzenberg, 1923: 140.



FIGS. 31–33. 31. *Pararhytida phacoides* n. sp., holotype, MNHN. Mt. Boulinda, sta. 97. 32. *Pararhytida pyrosticta* n. sp., holotype, MNHN. Mt. Tchingou, sta. 84. 33. *Pararhytida thyrophora* n. sp., holotype, MNHN. Ile Art, sta. 58. Scale line all 5 mm.

Holotype: S slope of Mt. Tchingou, 1250 m, rainforest. Coll. P. Bouchet, A. & S. Tillier, vii.1979 (sta. 84), MNHN (Fig. 32). Dimensions (mm): Shell height 8.0. Shell diameter 16.5. Aperture height 5.8. Aperture diameter 8.1. Umbilicus width 1.8. Whorls 5.1.

Paratypes (preserved): 5 + 6 juveniles, as above, MNHN (7 shells).

Other material: sta. 72(2), sta. 91(1), sta. 92(3).

Preserved material: 72, 84, 91, 92.

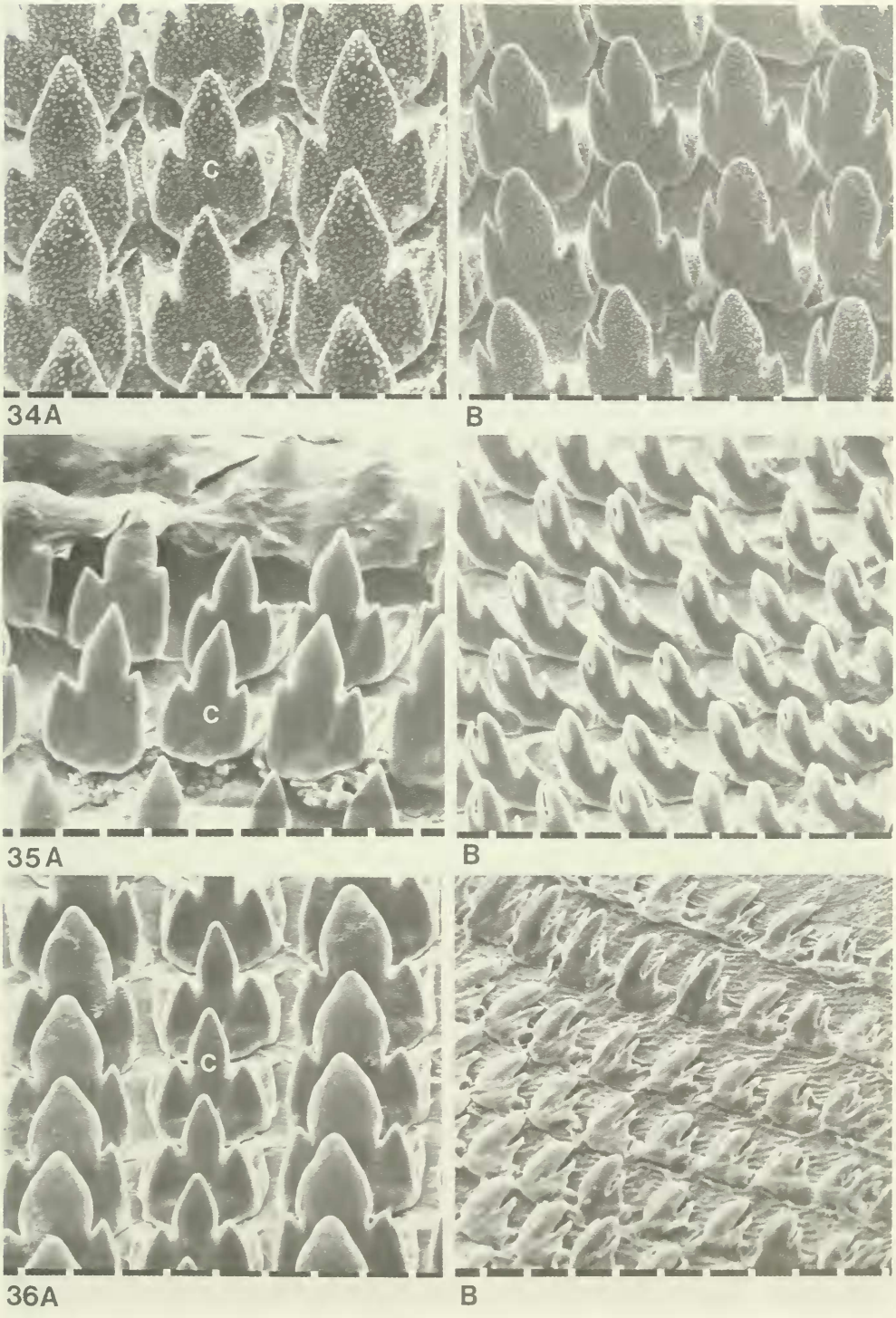
Etymology: with flame-like dots. Greek: pyr, fire; stictus, spotted.

Distribution

P. pyrosticta is restricted to very wet rainforests on the mountains of mainland New Caledonia N of the Houailou valley. This area corresponds to the northernmost part of the central chain together with the eastern slopes and summit areas of the Panié massif. At the stations from which it was collected rainfall ranges from 2500 to 3500 mm per annum.

Shell (Fig. 32)

The shell is similar to that of *P. phacoides*, being only slightly smaller and with fewer



FIGS. 34–36. 34A, central and lateral teeth; B, marginals. *Pararhytida phacoides* n. sp., Boulinda, sta. 97. 35A, central and lateral teeth; B, marginals. *Pararhytida pyrosticta* n. sp., Mt. Ignambi, sta. 72. 36A, central and lateral teeth; B, marginals. *Pararhytida thyrophora* n. sp., Ile Art, sta. 58. Scale divisions all 10 μm.

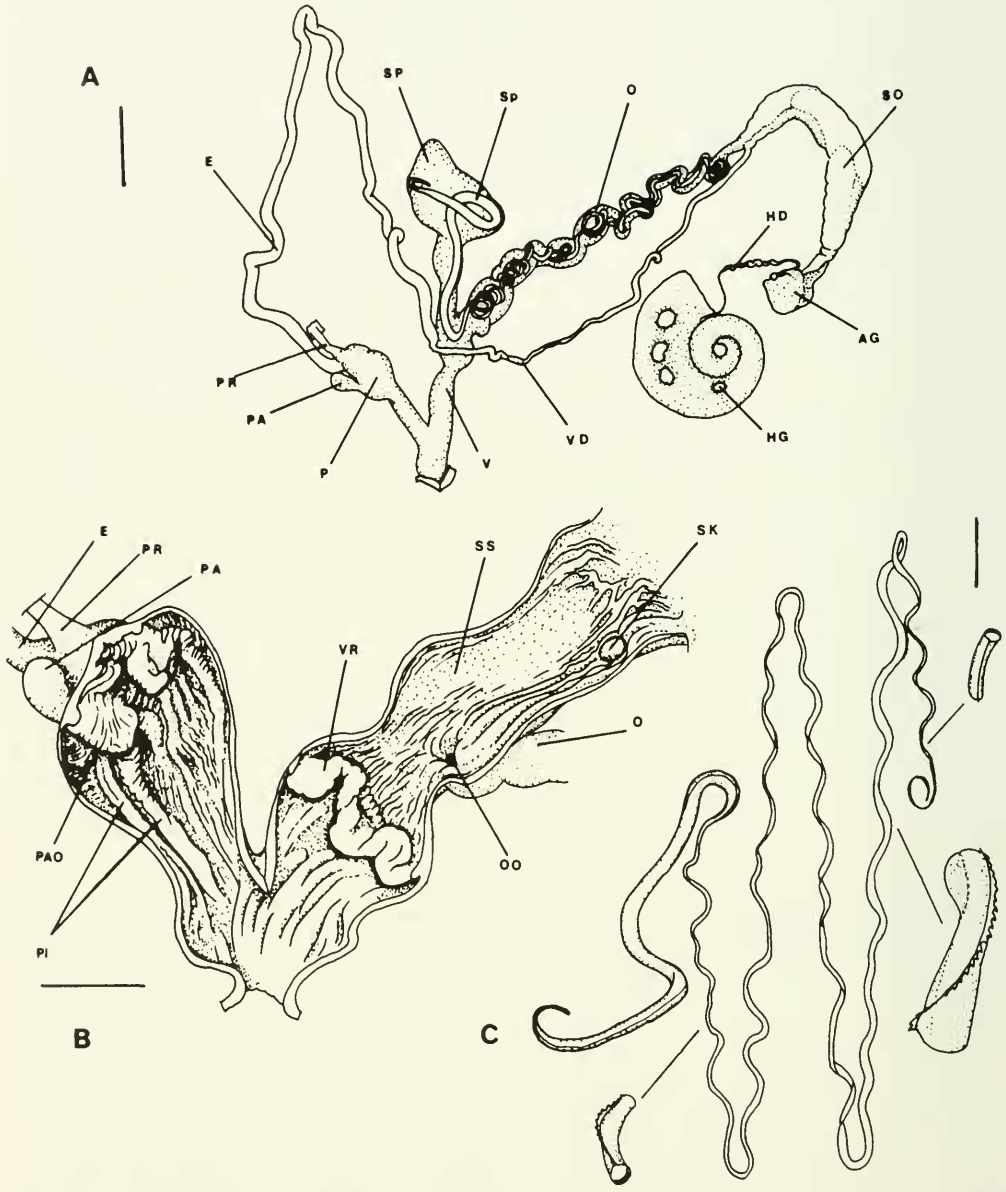


FIG. 37. Genital apparatus of *Pararhytida phacoides* n. sp., sta. 97. A, External morphology, indicating position of spermatophore. Scale line 5 mm. B, internal morphology. Scale line 2.5 mm. C, spermatophore. Scale line 2.5 mm. AG, albumen gland; E, epiphallus; HD, hermaphrodite duct; HG, hermaphrodite gland; O, oviduct; OO, oviducal opening; P, penis; PA, penial appendix; PAO, penial appendix opening; PI, penial pilasters; PR, penial retractor; SK, spermathecal knob; SO, spermoviduct; SP, spermatheca; Sp, spermatophore; SS, spermathecal stalk; V, vagina; VD, vas deferens; VR, vaginal ridge.

whorls when adult. Shells measure from 14.7 to 18 mm in diameter and from 7.3 to 8.4 mm in height, with an umbilicus from 1 to 1.9 mm in diameter. They have from 5 to 5.3 whorls on Mt. Ignambi (sta. 72) and Mt. Aoupinié (stas. 91, 92), but only between 4.7 and 5.1 whorls on Mt. Tchingou (sta. 84). Mean adult whorl count is 4.99 (s.d. 0.23).

Radula

Two radulae were examined (stas. 72 and 84, Fig. 35) and in both, the lateral teeth were distinctly narrower and sharper than in any other *Pararhytida* species. The mesocone of the central tooth also is narrow in comparison with species other than *P. thyrophora.* The number of teeth (Table 2) is about average for the smaller taxa.

Pulmonary complex

The lung cavity extends back 0.6 whorls on northern Mt. Ignambi (sta. 72), 0.75 whorls on the southern Aoupinié (stas. 91 and 92), and 0.8 to 0.9 whorls on the northwestern Mt. Tchingou (sta. 84). The rectal arm of the kidney is slightly longer than the cardiac arm; its absolute length is nearly constant, and thus it occupies more than ⅓ of the lung length in Mt. Ignambi, but less than ⅓ in Mt. Tchingou.

Genital apparatus

Externally, the genital apparatus of *P. pyrosticta* is characterised by a penis that is markedly shorter than the vagina, and by the size and shape of the spermatheca which has an ovoid head and a short, thick stalk (Fig. 38B).

Internally the penis has at most equally weak pilasters, and a small subapical verge in Mt. Tchingou specimens. All dissected specimens possessed an elongated vaginal appendage which is inserted above the midpoint of the vagina in Mt. Ignambi and Mt. Aoupinié specimens, and below it in specimens from Mt. Tchingou. The spermathecal knob is located just above the oviducal opening (Figs. 38C, D). In all specimens dissected the hermaphrodite gland has five lobes. The free oviduct is shorter at Mt. Tchingou than at the other two mountains.

Spermatophore: One complete spermatophore and some fragments were found in the Mt. Tchingou specimens. The complete spermatophore is very elongate, but without a differentiated tail, as in *P. mouensis* (Fig. 38A). The ridge is finely denticulated and extends around the imperforate extremity.

Discussion

P. pyrosticta looks externally very like *P. phacoides*, being only slightly smaller. In terms of genital anatomy the two species differ principally in spermatophore morphology, spermathecal shape, oviducal length, and internal penial and vaginal ornamentation.

Pararhytida thyrophora Mordan & Tillier, n. sp.
(Figs. 33, 36, 39)

Holotype: Ile Art, Belep Islands, N plateau. Coll. P. Bouchet and A. Warén, 7.vii.1979 (sta. 58). MNHN (Fig. 33). Dimensions (mm): Shell height 9.6. Shell diameter 18.3. Aperture height 6.7. Aperture diameter 9.1. Umbilicus width 1.7. Whorls 5.2.

Paratypes (preserved): 10 + 25 juveniles, as above, MNHN (+ 69 shells); 3 specs. BMNH Reg. no. 1984101; 3 specs., The Australian Museum, Sydney.

Other material: sta. 57(3).

Etymology: door-bearing. Greek: thyra, a door.

Distribution

P. thyrophora is known only from the Belep islands of Art and Pott. It was collected in dry, high maquis, where rainfall averages 1250 mm per year.

Shell (Fig. 33)

The shell ranges in size from 17 × 9 mm to 22.5 × 12.1 mm, with the umbilicus about 1 mm in diameter. The upper surface of the shell is more convex than in either *P. phacoides* or *P. pyrosticta*, but less than in some *P. mouensis*. The aperture is more rounded in adults than in juveniles, and the carina is situated about half way up the palatal wall. The number of whorls in the adult varies from 5.3 to 6.2 (mean 5.65; s.d. 0.19).

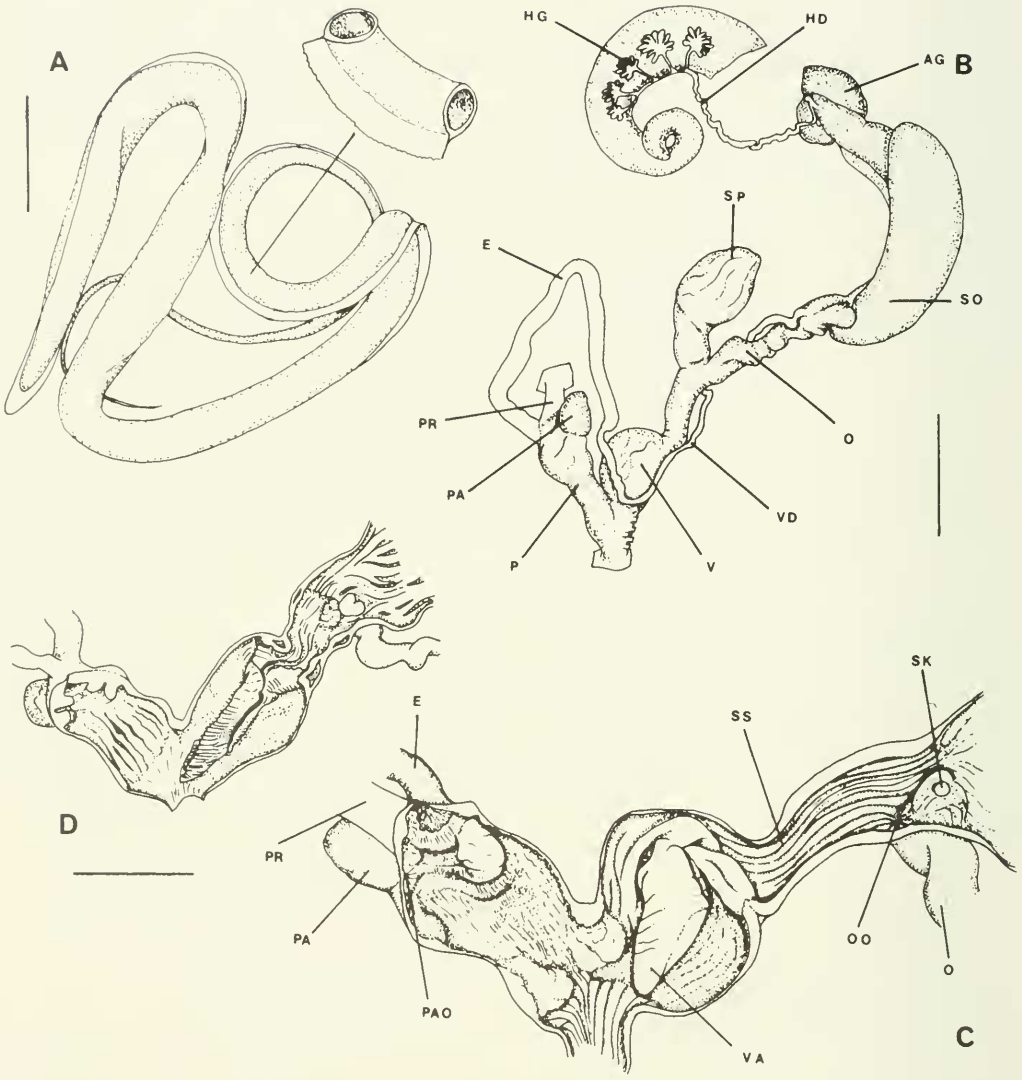


FIG. 38. Genital apparatus of *Pararhytida pyrosticta* n. sp., stas. 84 and 91. A, spermatophore, sta. 84, scale line 1.25 mm. B, external morphology, sta. 84, scale line 5 mm. C (sta. 84) and D (sta. 91), internal morphology, scale lines both 2.5 mm. AG, albumen gland; E, epiphallus; HD, hermaphrodite duct; HG, hermaphrodite gland; O, oviduct; OO, oviducal opening; P, penis; PA, penial appendix; PAO, penial appendix opening; PR, penial retractor; SK, spermathecal knob; SO, spermoviduct; SP, spermatheca; SS, spermathecal stalk; V, vagina; VA, vaginal appendage VD, vas deferens.

Radula

A single radula was examined from Ile Art (sta. 58, Fig. 36). It was characterised by the narrowness of the central tooth mesocone relative to the width of the entire tooth and relative to the mesocone of the laterals. The size and shape of the lateral teeth were normal for the small species of *Pararhytida*, but the number of teeth in each row (75) was higher.

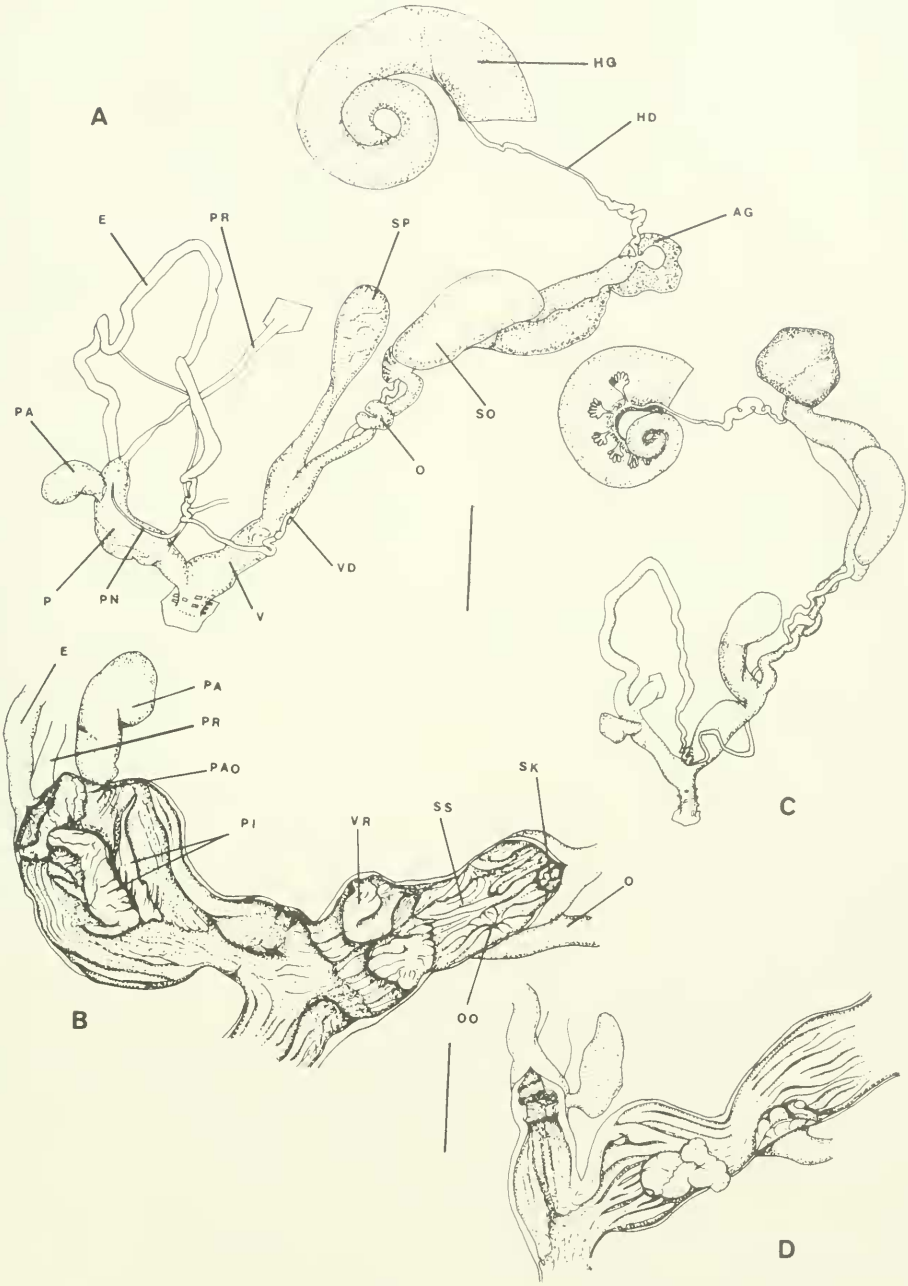


FIG. 39. Genital apparatus of *Pararhytida thyrophora* n. sp., stas. 57 and 58. A (sta. 58) and C (sta. 57), external morphology, scale lines both 5 mm. B (sta. 58) and D (sta. 57), internal morphology, scale lines both 2.5 mm. AG, albumen gland; E, epiphallus; HD, hermaphrodite duct; HG, hermaphrodite gland; O, oviduct; OO, oviducal opening; P, penis; PA, penial appendix; PAO, penial appendix opening; PI, penial pilasters; PN, penial nerve; PR, penial retractor; SK, spermathecal knob; SO, spermoviduct; SP, spermatheca; SS, spermathecal stalk; V, vagina; VD, vas deferens; VR, vaginal ridge.

Pulmonary complex

The lung cavity extends about 0.6 whorls in the dissected specimens (sta. 58). The rectal arm of the kidney is only slightly longer than the cardiac arm, and its length approaches one half of the lung length; only *P. dictyodes* has such a short lung, and no other species of *Pararhytida* has such a proportionally long kidney.

Genital apparatus

The penis is nearly as long as the vagina, and the free oviduct longer than the spermatheca (Figs. 39A, C). The shape of the latter is characteristic, with a pear-shaped head and a relatively thin stalk which is longer than the head. We were unable to count the lobes of the hermaphrodite gland accurately, but there were probably five or six.

Internally the penis has weak pilasters and a subapical verge at sta. 58 but not at sta. 57 (Figs. 39B, D), although in both cases the animals were fully mature. The vagina has an irregular transverse ridge which is almost developed into a full appendage. It is weaker than the appendage of *P. pyrosticta*, but better developed than in *P. phacoides*. It appears to be composed of two parts which partially interlock and occlude the vagina, and is situated at about the middle of the vaginal length. The spermathecal knob lies well above the oviducal opening, at about the mid-point of the spermathecal stalk. No spermatophore was found.

Discussion

The shell is more rounded in shape than any other small species, some *P. mouensis* excepted; in this last species, however, the shell is much thicker. In comparison with *P. marteli* the carination is less sharp and the apex more shallowly domed. Anatomically, the length and proportions of the pulmonary complex, and the shape of the spermatheca, allow easy species recognition. The insular situation of *P. thyrophora* makes the possibility of any significant gene flow with the mainland, and thus with other species of *Pararhytida*, seem highly unlikely.

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